EVOLUTION IN THE CONTEXT OF THE ENVIRONMENT

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A dissertation submitted to the faculty of the University of North Carolina at Chapel Hill in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Biology.

Chapel Hill
2009

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ABSTRACT

AMANDA JOAN CHUNCO: Evolution in the Context of the Environment
(Under the direction of Maria R. Servedio and Karin S. Pfennig)

Ecology can strongly influence evolution. To fully understand the evolutionary history of a species, it is essential to consider evolution within the context of the environment. Here, I explore how the environment produces different evolutionary patterns between populations and species, while considering how evolution in turn affects ecological patterns of distribution and population viability.

Within a single population, the environment can affect whether polymorphisms are maintained or lost. Using a population genetic model, I show how natural and sexual selection can result in the maintenance of male color polymorphisms (MCPs) in a single population. Specifically, I find that microhabitat heterogeneity can lead to MCP maintenance despite asymmetries in the strengths of natural and sexual selection and in microhabitat proportions. Also, while sexual selection alone is often sufficient for polymorphism maintenance, natural selection alone results in polymorphisms under only unrealistic conditions.

In comparing multiple populations, the environment influences population viability. When female mate choice is environmentally dependent, adaptive mate choice may affect the probability of population extinction. Here, I suggest how both the targets of mate choice and the fitness tradeoffs that females face influence extinction risk. I then describe how differential extinction risk in turn contributes to ecological patterns in

species distribution and community composition and macroevolutionary processes including speciation and species level selection.

Finally, I examined how the environment can influence range dynamics and species interactions in two spadefoot toad species. First, I used museum specimens to describe recent changes in species distribution. I found that these species have co-occurred in southern Arizona for at least 100 years. I also found that collection effort was more consistent in range interiors than at the periphery, making it difficult to interpret patterns of distribution at the range edge. Next, I used ecological niche modeling to determine how both abiotic and biotic factors contribute to species interactions. This work offers specific predictions that can be tested experimentally, while providing further evidence of the role of competition in driving species distributions. Together, these projects illustrate how both abiotic and biotic environmental factors dictate species distribution and abundance and thus potentially influence species interactions.

To my husband Marty, who has been a constant source of love and support and laughter and the best father a baby could ask for.

ACKNOWLEDGEMENTS

This work was not created in isolation, but reflects a great deal of support, of many different kinds, from a community of friends and colleagues. I first and foremost want to thank my committee. Karin Pfennig provided the academic freedom to pursue my own interests, while teaching me a great deal about using research to tell a compelling and broadly interesting story. Maria Servedio has been not only a great collaborator and teacher, but also a friend and valuable resource for advice on both career and family issues. The rest of my committee, including David Pfennig, Joel Kingsolver, and Aaron Moody, has been instrumental in helping me reach my professional goals by providing both a thoughtful critique of my work and broad training that will give me the flexibility to teach, do research, or both after I graduate.

My labmates, half labmates, office mates and grad school friends were a great source of research advice, feedback on talks and manuscripts, and more than anything else, emotional support and lots of fun. Ryan Martin, Amber Rice, Martin Ferris, Sarah Joseph, Jennifer Knies, Christy Violin, Sarah Diamond, Helen Ivarsson, Greg Ragland, and Cris Ledón-Rettig have been and continue to be amazing friends and the best part of grad school.

My family, both those related by blood and by marriage, have always been there for me when I needed them, and I feel incredibly lucky to have their love and support.

Finally, my husband, Martin Ferris, has been a constant source of support over the last five years. I would not have gotten through graduate school without him.

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CHAPTER I

INTRODUCTION

Understanding how the environment influences the evolution of a species is a fundamental goal of evolutionary ecology. The biotic and abiotic elements in any given environment define the ecology of the species that live there, and these elements play a major role in shaping the evolution of these species. Over short timescales, the environment can influence the distribution and abundance of a species. Over longer timescales, the distribution and abundance of a single species will affect other species in the community. These species interactions can result in potentially novel biotic environmental factors that will in turn have consequences for the evolution of the interacting species. Thus, considering the environment is essential to fully understanding both the evolutionary history and the evolutionary trajectory of a species.

Determining what specific effects the environment may have on populations is, however, a challenging task because the environment is rarely constant. Indeed, the spatial and temporal heterogeneity both within a habitat (i.e. microhabitat variation) and between habitats will strongly affect the selection pressures facing organisms within that environment. Habitat heterogeneity can influence evolution and ecology at multiple scales, from the existence of polymorphisms within a single population (Fuller et al. 2005), to more complex interactions between species across wide geographic ranges (Gaston 2003).

In this thesis, I consider the ecological and evolutionary consequences of environmental heterogeneity at multiple biological scales (both within and between species) as well as at multiple geographic scales (from microhabitats to species ranges). In doing so, my goal is to use multiple approaches to address questions about how the environment produces different evolutionary and ecological patterns between both populations and species.

Within even a single population, habitat variation can influence the evolutionary trajectory of that population. Indeed, spatial and temporal variation is an important explanation for the existence of phenotypic polymorphisms (Skúlason and Smith 1995). One example of phenotypic polymorphism is male color polymorphism (MCP). While male color polymorphisms are ubiquitous in nature (Barlow 1973; Anderson 1994; Hoffman and Blouin 2000), the maintenance of these polymorphisms is not yet fully understood. In Chapter 2, I use a population genetic model to investigate the specific environmental conditions that promote the maintenance of male color polymorphisms. In the model, I consider a single population with two male color morphs. This population is found in an area with two microhabitats. In one microhabitat, one morph is more conspicuous, while in the other microhabitat, the second morph is more conspicuous. This mimics a habitat that varies bimodally, such as aquatic habitats during morning vs. midday sunlight. Using this simple, but biologically plausible model, I can evaluate how habitat heterogeneity contributes to either polymorphism loss or maintenance. The results of this model are reprinted here with permission from the journal Evolution (Chunco et al. 2007).

Across populations, environmental heterogeneity can lead to divergent evolutionary paths, and may potentially lead to speciation or even differential extinction risk. In Chapter 3, I consider how environmental difference between populations can affect female mate choice, specifically in cases where individual fitness is improved at the cost of population level fitness (i.e. "Darwinian extinction", Houle & Kondrashov 2002; Webb 2003). As female mate choice is often dependent on the environment, environmental difference can result in divergent female mate choice preferences. For example, in high predation environments, females may alter their preferences in the presence of predators, while those from low predation environments do not (e.g. Godin & Briggs 1996). I suggest that when females in different habitats must make different tradeoffs in mate choice, populations can diverge, potentially resulting in differences in average fecundity and potentially population viability.

Across the range of an entire species, the distribution and abundance of a species will be determined by abiotic and biotic factors in the environment. Studying this phenomenon is becoming increasingly important as anthropogenic change is affecting the environments in which species live and interact, potentially resulting in entirely novel species interactions (e.g. Williams and Jackson 2007). In Chapter 4, I consider the effects of land-use change on the distribution and abundance of two species of spadefoot toads in the southwestern United States. Changes in agriculture, particularly cattle ranching, may have influenced these species because reproduction in both species is tied to ephemeral ponds that are often modified by ranchers. To capture historic patterns of when each species first arrived in the southwest, and to characterize how these species saturated this habitat after arrival, I used records from museum collections. Museum specimens are an

important source for historic data (Graham 2004), but I argue here that more systematic efforts at data collection and storage will be necessary to document the increasing effects of anthropogenic change.

Finally, at the level of multi-species interactions, the environment can influence whether species coexistence or competitive exclusion will occur in a given habitat. In Chapter 5, I use ecological niche modeling to look at the role of various abiotic and biotic factors in shaping distributions across the ranges of two species of spadefoot toads. Creating a model of predicted distributions of both species based on only abiotic factors provides a null distribution against which the effects of various biotic factors can then be tested. At the same time this work can be used to show where both are most likely to co-occur, providing targeted areas for future field studies.

Through this dissertation work, I aim to show some of the ways through which habitat variation can influence both evolutionary and ecological patterns, from the scale of the individual, to that of multi-species interactions.

REFERENCES

Anderson, M. 1994. Sexual selection. Princeton University Press, Princeton.

Barlow, G. W. 1973. Competition between color morphs of the polychromatic midas cichlid *Cichlosoma citrinellum*. Science 179:806-807.

Chunco, A. J., J. S. McKinnon, and M. R. Servedio. 2007. Microhabitat variation and sexual selection can maintain male color polymorphisms. Evolution 61: 2504-2515.

Fuller, R. C., K. L. Carleton, J. M. Fadool, T. C. Spady, and J. Travis. 2005. Genetic and environmental variation in the visual properties of bluefin killifish *Lucania goodei*. J. Evol. Biol. 18:516-523.

Gaston, K. J. 2003. *The structure and dynamics of geographic ranges.* Oxford University Press.

Godin, J.-G. & Briggs, S. E. 1996 Female mate choice under predation risk in the guppy. *Anim. Behav.* **51**, 117-130.

Graham, C. H., S. Ferrier, F. Huettman, C. Moritz, and T. Peterson. 2004. New developments in museum-based informatics and applications in biodiversity analysis. Tree 19: 497-503.

Hoffman, E. A. and M. S. Blouin. 2000. A review of colour and pattern polymorphisms in anurans. Biol. J. Linn. Soc. 70:633-665.

Houle, D. & Kondrashov, A. S. 2002 Coevolution of costly mate choice and condition-dependent display of good genes. *Proc. R. Soc. B* **269**, 97-104.

Skúlason, S. and T. B. Smith. 1995. Resource polymorphisms in vertebrates. Trends in Ecol. Evol. 10: 366-370.

Webb, C. 2003 A complete classification of Darwinian extinction in ecological interactions. *Am. Nat.* **161**, 181-205.

Williams, J. W. and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. Front. Ecol. Environ. 5: 475-482.

CHAPTER II

MICROHABITAT VARIATION AND SEXUAL SELECTION CAN MAINTAIN MALE COLOR POLYMORPHISMS

Abstract – Male color polymorphism may be an important precursor to sympatric speciation by sexual selection, but the processes maintaining such polymorphisms are not well understood. Here, we develop a formal model of the hypothesis that male color polymorphisms may be maintained by variation in the sensory environment resulting in microhabitat specific selection pressures. We analyze the evolution of two male color morphs when color perception (by females and predators) is dependent on the microhabitat in which natural and sexual selection occur. We find that an environment of heterogeneous microhabitats can lead to the maintenance of color polymorphism despite asymmetries in the strengths of natural and sexual selection and in microhabitat proportions. We show that sexual selection alone is sufficient for polymorphism maintenance over a wide range of parameter space, even when female preferences are weak. Polymorphisms can also be maintained by natural selection acting alone, but the conditions for polymorphism maintenance by natural selection will usually be unrealistic for the case of microhabitat variation. Microhabitat variation and sexual selection for conspicuous males may thus provide a situation particularly favorable to the maintenance of male color polymorphisms. These results are important both because of the general insight they provide into a little appreciated mechanism for the maintenance of variation

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in natural populations and because such variation is an important prerequisite for sympatric speciation.

Key Words – sympatric speciation, predation, habitat heterogeneity, female choice, model

INTRODUCTION

Polychromatism is widespread in nature (Barlow 1973; Anderson 1994; Hoffman and Blouin 2000; Gray and McKinnon 2006, 2007) and has long been central to studying the maintenance of variation within natural populations of animals (Ford 1965; Roulin 2004). Male color polymorphisms (MCPs), a type of polychromatism in which males within the same population exhibit different, discrete color morphs, is of particular interest both because of the role sexual selection may play in the evolution of such polymorphisms (Eakley and Houde 2004; Seehausen and Schluter 2004) and because MCPs may play an important role in sympatric speciation (Seehausen et al. 1999; Allender et al. 2003).

Several hypotheses have been proposed to explain the maintenance of MCPs. These include negative frequency dependent male-male competition (in cichlids, Seehausen and Schluter 2004), negative frequency dependent predation on male color morphs (in guppies, Olendorf et al. 2006) a balance between female preference and male aggression (in swordtails, *Xiphophorus pygmaeus,* Kingston et al. 2003), female preferences for unfamiliar or novel males (Hughes et al. 1999; Eakley and Houde 2004; Kokko et al. 2007), and spatial and temporal habitat heterogeneity (Fuller et al. 2005). As male color is potentially selected on by both predators and females, both types of receivers must be considered to explain the maintenance of MCPs within a population;

predation often favors inconspicuous traits, while sexual selection often favors conspicuousness (Endler 1980; Anderson 1994; Zuk and Kolluru 1998).

Given that signal perception is highly habitat dependent (Endler 1980; Bradbury and Vehrencamp 1998; Chiao et al. 2000), it is impossible to interpret the signal outside the context of the environment. Color perception depends on the properties of the signal, the light under which the signal is perceived, the background against which it is viewed, the medium through which the signal is sent (i.e. air or water), and the sensory capabilities of the receiver (Endler 1991; Chiao et al. 2000; Endler and Mielke 2005). Therefore, if an environment is heterogeneous in substrate type, light intensity, or other factors that influence signal perception, the potential exists for several different color morphs to persist, as each morph will represent the optimal balance between natural and sexual selection within a given visual microhabitat (Gamble et al. 2003). Indeed, empirical evidence that habitat variation affects signal conspicuousness and the evolution of male signals has now been obtained for several sensory systems from diverse taxa including birds, lizards, frogs, insects, and fish (for a review, see Boughman 2002).

Although empirical evidence suggests a role for fine scale habitat variation in the maintenance of MCPs, a formal theoretical analysis of how differential selection between microhabitats may lead to the maintenance of male color polymorphisms has not previously been developed. Here we present a population genetic model that looks at the conditions under which habitat heterogeneity in qualities affecting color perception will lead to the existence of a stable male color polymorphism. In so doing, we answer three specific questions about the likelihood of this mechanism maintaining a polymorphism in natural populations: 1) Can MCPs be maintained by either natural selection or sexual

selection alone? 2) How robust are the conditions for MCP maintenance to asymmetries in habitat frequencies and selection strengths? and 3) How does changing the biological assumptions of the conditions under which selection occurs, for both natural and sexual selection, influence the outcome of the model? Although we focus throughout on MCP's as our 'case study', our goal is to develop a relatively general model of how environmental variation might contribute to the maintenance of variation in signals. For this reason, we keep our model of signal conspicuousness relatively simple and general.

THE MODEL

In this haploid model, we consider a population of sexually dimorphic animals. Males are polymorphic for color with two distinct morphs. For convenience, we refer to them here as blue (occurring with frequency p_b) and yellow (occurring with frequency p_y). These color patterns are common in fish MCPs (e.g. Seehausen and Schluter 2004; Gray and McKinnon 2006) and are also seen in lizards (e.g. Sinervo and Lively 1996). A great deal of work has been done on the genetic basis of blue and yellow color polymorphisms, and in several of these systems, color expression is controlled in large part by a single locus with multiple alleles (in swordtails, *Xiphophorus pygmaeus*, Baer et al. 1995; in killifish, *Lucania goodei*, Fuller and Travis 2004; in side-blotched lizards, *Uta stansburiana*, Sinervo and Zamudio 2001). Therefore, we modeled color as being controlled by a single locus with two alleles. We assume that females are monomorphic for color and that color is entirely genetically controlled in both sexes. Although color does not indicate genetic or phenotypic quality, it does affect fitness in

that males that are more conspicuous within their environment are both more vulnerable to predation and more likely to be chosen by females.

The habitat in which natural and sexual selection occurs is divided into microhabitats that differ in physical properties that influence color perception, such as light intensity, light spectrum, and/or substrate color and pattern. Because of these differences in visual properties, each microhabitat provides a functionally different setting within which male color is perceived by females and by predators. Environmental heterogeneity encountered by an individual is not the result of migration; rather, variable visual backgrounds within the general environment result from fine-scaled spatial or temporal differences (e.g. Gamble et al. 2003).

We specifically consider an environment with two microhabitats. The blue male color morph is more conspicuous than the yellow male morph in habitat H_b (occurring with frequency h_b), while in habitat H_y (occurring with frequency $h_y = 1\text{-}h_b$), the reverse is true. Both sexes move freely and randomly between habitats (neither males nor females actively choose a habitat) so that each sex has a probability of being in each microhabitat according to relative habitat area.

The life cycle begins with the zygote stage. Natural selection follows birth and acts exclusively on males. The more conspicuous morph in each microhabitat suffers a greater loss from predation. Specifically, s_b represents the selection coefficient against blue males in habitat H_b, while s_y is the selection coefficient against yellow males in habitat H_y. Because habitat varies on a small (microhabitat) scale, we model natural selection as occurring across habitats that organisms can freely move between (see Dempster 1955). Therefore, in males, the absolute fitness of the blue morph from natural

selection (superscript "*ns*") is $w_b^{ns} = h_b(1 - s_b) + h_y$, which simplifies to $w_b^{ns} = 1 - h_b s_b$, and the absolute fitness of the yellow morph is likewise $w_y^{ns} = 1 - h_y s_y$. The frequency of the blue morph (p_b) after males undergo natural selection (p_b^*), is given by equation 1:

$$p_b^* = \frac{p_b w_b^{ns}}{p_b w_b^{ns} + p_y w_y^{ns}}. \quad (1)$$

Since females do not express the color alleles, the frequency of the blue allele carried by females at this stage of the life cycle remains p_b .

After natural selection, mating (sexual selection) occurs. We assume a polygynous system where females have equal mating success (e.g. Kirkpatrick 1982) and males provide no resources to females other than their genetic contribution. The sole advantage males of each color possess over differently colored competitors is their microhabitat-dependent conspicuousness. This advantage is represented by a factor a_i (where $i = b$ or y depending on the microhabitat that the female is in), where females are a_i times more likely to mate with a more conspicuous morph than a less conspicuous morph if they encounter one of each. For now, we assume that females choose between blue and yellow males within their current microhabitat. That is, females are either in habitat H_b or H_y when mating decisions are made, and they can only view one background at a time. Mating success of each male morph is thus determined separately within each habitat (see Levene 1953).

The proportion of each type of cross is shown in the mating table (Table 1). Here, the mating table is a matrix $\mathbf{M}_{ij}$, where i represents female type in each habitat (i.e. row

number in Table 1) and *j* represents male type in each habitat (i.e. column number in Table 1). The frequency of the blue color allele in the following generation ($p_b(t+1)$) is shown by equation 2:

$$p_b(t+1) = M_{11} + \frac{1}{2}M_{13} + M_{22} + \frac{1}{2}M_{24} + \frac{1}{2}M_{31} + \frac{1}{2}M_{42}. \quad (2)$$

The final recursion can be obtained by substituting the appropriate values of the cells of Table 1 into equation (2). Equilibrium frequencies were found by setting the offspring frequencies at time *t* equal to the frequencies at time *t*+1 and solving the resulting recursion equation.

RESULTS

Three equilibria result from this model. Two of the equilibria represent loss ($\hat{p}_b = 0$) and fixation ($\hat{p}_b = 1$) of the blue color morph. The third equilibrium is polymorphic. The best way to understand the polymorphic equilibrium from the full model is to first present the equilibrium under sexual selection alone (with no natural selection, $s_b = s_y = 0$). We are interested in the polymorphic equilibrium frequency of the blue morph, $\hat{p}_b$, so we write the relative fitness of blue males, due to sexual selection alone (superscript "ss"), as $w^{ss}_{b,Hb} = a_b$ in the habitat where blue is conspicuous (H_b) and as $w^{ss}_{b,Hy} = 1/a_y$ in the habitat where yellow is conspicuous (H_y) (the relative fitness of yellow males in habitat H_y must also be rescaled throughout the results below to 1 instead of a_y, changing

the normalization factor v in the mating table to $w^{ss}_{b,Hy}p_b + p_y$). We can then express the polymorphic equilibrium, due to sexual selection alone, as

$$\hat{p}_b = -\frac{h_b(w^{ss}_{b,Hb} - 1) + h_y(w^{ss}_{b,Hy} - 1)}{(w^{ss}_{b,Hb} - 1)(w^{ss}_{b,Hy} - 1)}. \quad (3)$$

The term $(w^{ss}_{b,Hb} - 1)$ is a measure of the selection coefficient favoring the blue morph due to sexual selection in habitat H_b (this term will be positive since a_b>1), while $(w^{ss}_{b,Hy} - 1)$ represents the parallel selection coefficient against the blue morph in habitat H_y (this term will be negative since a_y>1). Equation (3) therefore shows that the polymorphic equilibrium frequency of the blue allele due to sexual selection alone is a balance between the frequency of habitat H_b times the selection coefficient favoring blue in that habitat, and the frequency of habitat H_y times the selection coefficient against blue in that habitat, scaled by the product of the selection coefficients (the minus sign in front of equation (3) can be thought of as correcting for the negative selection coefficient in the denominator).

To look at the equilibrium under the full model, we can simply replace the fitnesses of the blue morph in equation (3) with ones that represent the action of both natural and sexual selection (superscript "*tot*"). Therefore,

$$\hat{p}_b = -\frac{h_b(w^{tot}_{b,Hb} - 1) + h_y(w^{tot}_{b,Hy} - 1)}{(w^{tot}_{b,Hb} - 1)(w^{tot}_{b,Hy} - 1)} \quad (4)$$

where $w_{b,Hb}^{tot} = A_b$ and $w_{b,Hy}^{tot} = 1/A_y$, and where

$$A_b = \frac{a_b w_b^{ns}}{w_y^{ns}} \text{ and } A_y = \frac{a_y w_y^{ns}}{w_b^{ns}}.$$

A_i is therefore equal to the strength of female preference, a_i, for a color morph when it is conspicuous, multiplied by the ratio of the fitnesses due to natural selection of the conspicuous to the inconspicuous morph.

Stabilities of the equilibria were determined using a linear stability analysis. The equilibrium $\hat{p}_b = 1$ (that is, the fixation of the blue morph) will be unstable when

$$\lambda_{p1} = \frac{1}{2}\left(1 + \frac{h_b}{w_{b,Hb}^{tot}} + \frac{h_y}{w_{b,Hy}^{tot}}\right) > 1 \qquad (5)$$

and the equilibrium $\hat{p}_b = 0$ (that is, the loss of the blue morph) will be unstable when

$$\lambda_{p0} = \frac{1}{2}\left(1 + h_b w_{b,Hb}^{tot} + h_y w_{b,Hy}^{tot}\right) > 1. \qquad (6)$$

The eigenvalue λ_{p1} consists of terms describing the contributions by females and males to increases in the frequency of the yellow morph, which is the potentially invading morph when blue is fixed (i.e. $\hat{p}_b = 1$), as follows. The factor of ½ is present because there are separate contributions to the eigenvalue from each sex. Color in females is neutral, so the

contribution from females is 1. The following two terms, $h_b / w^{tot}_{b,Hb}$ and $h_y / w^{tot}_{b,Hy}$ represent contributions from males in habitat H_b and males in habitat H_y respectively, scaled by the relative fitnesses of the yellow morphs (the reciprocal of the fitnesses of the blue morph) in each respective habitat. Likewise, the eigenvalue λ_{p0} consists of contributions by females and males to the spread of the blue morph, the potentially invading morph when the yellow morph is fixed (i.e. $\hat{p}_b = 0$), where $h_b w^{tot}_{b,Hb}$ and $h_y w^{tot}_{b,Hy}$ represent contributions from males in each habitat scaled by the relative fitness in that habitat of the blue morph.

Note that our solutions to this point elaborate upon the findings of Gliddon and Strobeck (1975). Using our equation (4), we can write an equation for Δp_y (where $p_y = 1 - p_b$),

$$\Delta p_y = \tfrac{1}{2} p_b p_y \left(\frac{h_b (w_{y1} - 1)}{1 + p_y (w_{y1} - 1)} + \frac{h_b (w_{y2} - 1)}{1 + p_y (w_{y2} - 1)} + \frac{h_y (w_{y3} - 1)}{1 + p_y (w_{y3} - 1)} + \frac{h_y (w_{y4} - 1)}{1 + p_y (w_{y4} - 1)} \right). \quad (7)$$

This is equivalent to equation (1) in Gliddon and Strobeck (1975) when $w_{y1} = 1/w^{tot}_{b,Hb}$, $w_{y2} = 1$, $w_{y3} = 1/w^{tot}_{b,Hy}$, and $w_{y4} = 1$ correspond to the fitnesses of the yellow morph in males in habitats H_b (for w_{y1}) and H_y (for w_{y3}) and females in habitats H_b (for w_{y2}) and H_y (for w_{y4}). Equation (7) contains a factor of ½ to account for the fact that sexual selection is treated separately in each sex. Gliddon and Strobeck's (1975) stability conditions (2) and (3), applied to equation (7) correspond exactly to our eigenvalues λ_{p1} and λ_{p0} respectively.

The polymorphic equilibrium will be stable when both conditions (5) and (6) hold. If we make the appropriate substitutions for the w_b^{tot} terms, we can see that condition (5) is more likely to hold (the equilibrium $\hat{p}_b = 1$ is more likely to be unstable and yellow is more likely to invade) with lower sexual selection favoring the blue morph (a_b), higher sexual selection favoring the yellow morph (a_y), and higher fitness due to natural selection of the yellow versus blue morph ($s_y < s_b$). The opposite conditions will tend to promote instability of the $\hat{p}_b = 0$ equilibrium and therefore the invasion of the blue morph into a population of yellow individuals. When the appropriate balance is reached in the strength of the natural and sexual selection parameters, given a specific ratio of the habitats to one another, the polymorphic equilibrium will be maintained.

Although equation (4) and the conditions that follow from equations (5) and (6) present analytical solutions to the model and an intuitive feel for the effects of the parameters, we examine several cases graphically and numerically in order to illustrate the conditions for stability in an easily interpretable manner. This is done using the analytical results, not by separate simulations.

To illustrate the results when both natural and sexual selection are acting, we began with the assumption that the strengths of natural selection and sexual selection are symmetrical for blue and yellow morphs ($s_b = s_y$ and $a_b = a_y$). Under these assumptions, we find that the polymorphic equilibrium is stable under a broad range of conditions (Fig. 1). The values of preference and selection that result in a stable polymorphism are most restricted when the habitats are highly skewed, but are more permissive as habitats become more symmetrical. When habitats are exactly symmetrical ($h_b = h_y = .5$) in addition to the symmetry in natural and sexual selection, a stable polymorphism results

regardless of the values of selection and preference. Again, however, even highly skewed habitats can lead to a stable polymorphism with strong female preferences.

To illustrate the results when natural selection, sexual selection, and habitat frequency deviated from symmetry, we found the eigenvalue at each of the three equilibria (0, 1, and the polymorphic equilibrium; for the latter see (5) and (6)), solved for a_y, and then substituted specific values of s_b, s_y, h_b, h_y and a_b into the resulting expression. This allowed us to see what range of asymmetry in sexual selection strengths is permissible to maintain the polymorphic equilibrium, given a set of parameter values. In doing these tests, we evaluated a wide range of values for natural selection, sexual selection, and habitat frequencies (s: 0.01-0.99; a_b: 0-infinity; h: 0.01-0.99) for 60 unique combinations of parameters. Representative examples of the outcomes of different selection scenarios are presented in Table 2. We found that the polymorphic equilibrium was generally stable over a range of parameter values (Table 2), however, when the starting parameters were highly asymmetric, the range of parameter space leading to a stable polymorphism could be quite restricted.

Finally, we evaluated a scenario where the morph favored by females also suffered lower predation than the less favored morph (s_b and $s_y < 0$). This could result if females favored more cryptic morphs. In this case, a stable polymorphism was again possible, although the conditions resulting in a stable polymorphism show slight numerical differences from cases with comparable selection strengths where female preferences and natural selection favored different morphs (Table 2).

It is also illustrative to examine the effects of natural and sexual selection alone in this model. To look at sexual selection alone, we removed natural selection ($s_b = s_y = 0$).

In this case, predators act indiscriminately, while females still preferentially choose conspicuous males. Our polymorphic equilibrium for this scenario is shown in equation (3), and the conditions for stability can be seen by setting $s_b = s_y = 0$ in the eigenvalues (5) and (6) above, which yields a stable polymorphic equilibrium when

$$\lambda_{p1} = \frac{1}{2}\left(1 + \frac{h_b}{a_b} + a_y h_y\right) > 1 \text{ and } \lambda_{p0} = \frac{1}{2}\left(1 + h_b a_b + \frac{h_y}{a_y}\right) > 1 .$$

Again, we can see that a stable polymorphism will be likely when a balance is struck between the strengths of sexual selection and the habitat frequencies.

Under these conditions, female preference is often sufficient to maintain a polymorphism. When preferences are symmetrical between habitats ($a_b = a_y$), even slight female preference (i.e. $a = 1.01$) will maintain a polymorphism, although this requires that habitat frequencies are also close to symmetrical ($h_b \approx h_y$). As the strength of a symmetrical female preference increases, a polymorphism will be maintained under increasingly wide degrees of habitat asymmetry (Fig. 2a). The specific frequency of the blue morph under different conditions of habitat frequency and strength of preference is seen in Figure 2b. When we do not assume symmetry between female preference in each habitat ($a_b \neq a_y$), we find that a stable polymorphism is maintained under the widest range of frequencies when habitats are close to symmetrical, with increasing strength of preferences needed to maintain a polymorphism as habitat becomes increasingly skewed (Fig. 2c). Additionally, when habitat frequencies are symmetrical, a polymorphism is maintained when preferences are close to symmetrical; however, as asymmetry in habitat

frequencies increases, a corresponding skew in preference strength (with stronger preferences for the morph favored in the rarer habitat) is required to maintain a polymorphism. Even under highly skewed conditions, however, a polymorphism will occur if the strength of preference for the conspicuous morph in the rarer habitat is strong enough.

We next looked at the outcome of natural selection alone (modeled here as occurring across habitats, as described above) by removing the effects of sexual selection (s_b, $s_y > 0$; $a_b = a_y = 1$). In this scenario, predators preferentially prey upon conspicuous morphs, while females mate randomly. In this case, a polymorphism resulted only when there were exactly symmetrical parameters between habitats ($s_b = s_y$, $h_b = h_y$) or when selection and habitat area are exactly balanced. Any deviation from these conditions leads to the fixation of either the blue or the yellow morph. These conditions of complete symmetry are highly unrealistic and unlikely to occur in nature. This result is unsurprising because several authors have demonstrated the difficulty of maintaining a polymorphism when selection occurs across habitats, as we have modeled natural selection here (eg. Dempster 1955; Christiansen 1975; Karlin and Campbell 1981; de Meeûs et al. 1993).

ALTERNATIVE ASSUMPTIONS

In the model above, we consider the maintenance of a color polymorphism when natural selection is assumed to occur across habitats (males of both morphs move between habitats), whereas sexual selection occurs within habitats (females choose among the males that are present in the microhabitat that the female happens to be in

when she is ready to mate). To confirm the effects of these assumptions on the outcome of the model, we also examined the outcome of selection when we considered alternative assumptions. That is, we modeled natural selection as occurring within one habitat (males remain in one microhabitat throughout the period of natural selection and potentially subsequent reproduction and predators stay within a habitat at least for each prey selection event) and we modeled sexual selection occurring across habitats (females examine males in both habitats before they choose a mate). In the discussion below, we describe when these alternative assumptions may be appropriate.

To look at natural selection occurring within habitats, we use the notation w_i^{ns}, where *i* is *b* or *y*, to denote fitness of the blue and yellow morphs. Here, in habitat H_b, the fitness of the blue morph is $w_{b,Hb}^{ns} = 1 - s_b$ and the fitness of the yellow morph is $w_{y,Hb}^{ns} = 1$. In habitat H_y, where the yellow morph is conspicuous, the fitness of the blue morph is $w_{b,Hy}^{ns} = 1$ and the fitness of the yellow morph is $w_{y,Hy}^{ns} = 1 - s_y$. After natural selection, the frequency of the blue morph in microhabitat *i* is now

$$p_{b,Hi}^{*} = \frac{p_b w_{b,Hi}^{ns}}{p_b w_{b,Hi}^{ns} + p_y w_{y,Hi}^{ns}} \tag{8}$$

where *i* is *b* or *y* depending on the microhabitat. When combining the frequencies across habitats, we must take into account the proportion of each microhabitat, so the total frequency of the blue morph is $p_b^{*} = p_{b,Hb}^{*} h_b + p_{b,Hy}^{*} h_y$. This combination of the frequencies multiplied by the proportion of each habitat is valid in two cases: 1) if there is reproduction with separate population regulation in each habitat (see Levene 1953), or 2)

if the population density of our focal species between each habitat remains equivalent because of equivalent densities of a species of predator. Solving for the equilibrium condition for natural selection alone with these assumptions yields three equilibria (0, 1, and a polymorphic equilibrium). This polymorphic equilibrium is

$$\hat{p}_b = -\frac{h_b\left(g_{b,Hb}-1\right)+h_y\left(g_{b,Hy}-1\right)}{\left(g_{b,Hb}-1\right)\left(g_{b,Hy}-1\right)}, \tag{9}$$

where $g_{b,Hb} = \frac{w^{ns}_{b,Hb}}{w^{ns}_{y,Hb}}$ and $g_{b,Hy} = \frac{w^{ns}_{b,Hy}}{w^{ns}_{y,Hy}}$. Note that the structure of equation (9) is exactly parallel to that of equation (3) above, and can be explained by the same logic. The stability conditions for these equilibria are also parallel to the results of the full model above (equation 4 and see Gliddon and Strobeck 1975). Under these conditions, polymorphism maintenance by natural selection alone is therefore quite possible. However, if microhabitat variation is truly on a small scale, the assumption that males will remain in any given microhabitat throughout the time that prey is likely to be under selection (or that the effects of predation on population density in each habitat would be exactly equivalent) is probably unreasonable except for certain organisms with very specific patterns of dispersive and non-dispersive life history stages, and predators with appropriate foraging behavior.

We next considered sexual selection occurring across habitats. In this situation, females view all males across both habitats before selecting a mate. Therefore, the mating table **F** is a 2x2 matrix with only two female types (females carrying the blue allele and females carrying the yellow allele) and two male types (blue males and yellow males).

The mating table is shown in Table 3. The frequency of the blue color morph in the following generation ($p_b(t+1)$) is shown by equation 10:

$$p_b(t+1) = F_{11} + \frac{1}{2}F_{12} + \frac{1}{2}F_{21}. \quad (10)$$

The final recursion can be obtained by substituting the appropriate values of the cells of Table 3 into equation (10)**.** When sexual selection is modeled with these assumptions, the only equilibria that result are loss ($p_b = 0$) and fixation ($p_b = 1$) of the blue color morph. Here, we can think of the loss of polymorphism occurring because sexual selection is unidirectional. Specifically, since females sample both habitats before mating, there is only one set of conditions that all females experience. Therefore, one particular male morph will generally be more attractive to females than the other and will receive a higher proportion of matings. This contrasts with within microhabitat selection because when females only view males from one microhabitat before mating, some females will prefer blue males and some will prefer yellow males, depending on the habitat that they are in when they make their choice. In this scenario, sexual selection will be divergent between habitats and thus more likely to lead to a polymorphism.

DISCUSSION

It has long been known that a heterogeneous environment can be important in maintaining phenotypic and genetic variation. Previous models, however, have generally found that polymorphism maintenance in a heterogeneous environment is either quite restricted (e.g. Dempster 1955) or requires population regulation to occur separately in

each habitat (e.g. Levene 1953). The model we present above differs in two important ways – 1) we include habitat dependent sexual selection and 2) the scale at which selection occurs is quite small, so that each individual may experience several habitats, even within the course of the day. We find that including sexual selection in a model of microhabitat variation, either as the sole selective force or in conjunction with natural selection, can often lead to a stable polymorphism.

In our initial model of natural selection occurring across habitats and sexual selection occurring within habitats, we find that natural selection alone cannot maintain a polymorphism, but sexual selection can, either alone or in conjunction with natural selection. This is because in our initial model, natural selection can be thought of as being subsumed by sexual selection. For example, from the males' perspective, increasing the probability of survival is mathematically equivalent to increasing the mating success of that male in both habitats; changes in natural selection thus have effects that can be described within the context of the sexual selection model. Although natural selection alters the relative fitness of each type of male, as long as some males of each color survive, polymorphism maintenance will ultimately be determined by the fact that reproductive fitness is essentially regulated separately by female choice in each habitat (see equations 3 and 4).

Our findings stem from the assumptions that we make regarding whether natural selection and sexual selection are occurring within or across habitats. By selection within habitats, we refer to the case where females or predators select males only from within the habitat that they (the agents of selection) are currently in, while selection across habitats refers to the scenario of females or predators sampling different habitats before

finally selecting a male. With natural selection, in the former case we also assume that males stay within habitats throughout the entire period of selection, whereas in the latter case, we assume that males are moving in between habitats between individual predation events as well. Here, we can think of selection occurring within habitats as being roughly analogous to soft selection, as the processes regulating the population are occurring separately in each habitat. In contrast, selection occurring across habitats is roughly analogous to hard selection, because the processes regulating the population occur on a larger scale that spans both habitats. Under hard selection, the contribution of organisms to the next generation is absolute regardless of habitat, whereas under soft selection, organisms from each habitat contribute to the next generation in proportion to the carrying capacity of that habitat (Karlin and Campbell 1981). Previous models of hard selection find that the conditions for polymorphism maintenance are quite restrictive, while models of soft selection find that polymorphisms can be maintained under a much broader range of conditions (Christiansen 1975; Karlin and Campbell 1981; de Meeûs et al. 1993). We see a similar outcome in our model, where selection occurring within habitats is more conducive to polymorphism maintenance than selection occurring across habitats.

When we model sexual selection as occurring within habitats in our primary model, we find broad conditions for polymorphism maintenance. Because the mating success of females is not dependent upon the habitat in which they choose mates, females will contribute offspring to the next generation in ratios proportional to the habitat ratios themselves. Sexual selection under these assumptions thus provides a form of independent population regulation within each habitat. In contrast, we show that an

across habitat sexual selection model cannot maintain a polymorphism. The conditions under which female choice occurs will determine whether modeling sexual selection as occurring within or across habitats is more appropriate. If a female chooses from among the males that are present in the habitat that the female happens to be in when she decides to mate, then modeling selection as occurring within each habitat is most appropriate. This could occur if the patch size is large or if the habitat type is temporal (perhaps with daylight changes over the course of the day). Alternatively, if females move between habitats as they evaluate potential mates, modeling sexual selection as occurring across habitats may then be the more appropriate assumption. If costs associated with searching for a mate are high, the latter situation may be less common because it requires females to view males from both habitats before making a mating decision.

Our results highlight the potential importance of sexual selection, in this case for conspicuous male traits, in maintaining a stable polymorphism. The conditions for polymorphism maintenance under sexual selection can often be broad. We found symmetry of parameter values between habitats to be very important in determining the range of parameter space that will lead to a stable polymorphism. When sexual selection, natural selection and habitat frequency are completely symmetrical between habitats, polymorphism is the only possible outcome. As symmetry decreases, the parameter space that leads to a polymorphism decreases as well, although not particularly rapidly. When parameters are highly skewed between habitats, a stable polymorphism is still possible, although the range of female preferences that will yield a polymorphism may be quite restricted (see Table 2). Thus polymorphism maintenance does not require symmetry, but in cases where equilibrium frequencies in traits are expected to be highly asymmetric,

stochastic forces acting in natural populations may be expected to lead to the loss of the less common allele.

The stable polymorphism maintained under sexual selection results because under certain sets of parameter values, the rare morph in the population will increase in frequency. We can think of the habitat under these conditions as essentially having "protected areas" that result from a combination of microhabitat area and female preference. In some areas (or microhabitats), one morph is favored, while in different areas, the other morph is favored. Under conditions where the polymorphism is stable, the increase in frequency that a rare morph will exhibit in the areas where it is favored will more than compensate for the decrease in frequency that it will experience in areas where it is not favored. For example, when habitat frequency and preference strengths are symmetrical and only sexual selection is acting, half the females in a population will prefer blue males and half will prefer yellow males at any given time. Therefore, if a morph frequency falls below 50%, the rarer morph will have a mating advantage. By analogy with models of feeding polymorphisms, the rare male morph can be thought of as having more of its favored resource, the habitat in which it is more conspicuous and preferred by females, available to it. This mechanism, which is usually defined as a form of spatially varying selection (e.g. Futuyma 1997), behaves very similarly to frequency dependence in terms of the advantages gained by a rare morph. Frequency dependence is not, however, explicitly included in our equations (our selection coefficients s and a are constants and do not depend upon the frequency of the color morphs in the population). Because of the general nature of the mechanism of polymorphism maintenance, we

expect the qualitative results to be robust to changes in many of our specific assumptions such as ploidy levels or the absence of sexual dimorphism.

In our primary model, we treat natural selection as occurring across habitats, and conclude that, as expected, a polymorphism cannot be maintained under these conditions when natural selection acts alone. We additionally assess the result of modeling natural selection as occurring within habitats, as in soft selection, in one of our alternative models; we find that a stable polymorphism can indeed be maintained, even when parameters are not symmetrical (e.g. Levene 1953; Christiansen 1975; de Meeûs et al. 1993; see Dempster 1955). Which of these assumptions is more appropriate depends to some degree on the biology of a particular situation. It is generally assumed that when organisms can move freely between habitats, as would be the case with the microhabitats modeled here, treating selection as occurring across habitats is more realistic (e.g. Dempster 1955). This could occur if predators move between habitats during a prey selection event and view males against different backgrounds before choosing a prey item. This may be especially likely if predators have a large body size relative to that of the prey species. More importantly, we assume that males are freely moving between selection events when selection is occurring across habitats. Thus, as predators remove selected males, the frequency of each morph changes in both habitats, regardless of where the predation took place.

If our alternative, within habitat, model of natural selection is to be appropriate, we need to assume that predators stay within a habitat during each specific predation event, at a minimum, and males remain in a specific microhabitat during the entire set of prey selection events. Moreover, to match our specific within-habitat assumptions,

predators would be assumed to disperse randomly to microhabitats, rather than spending more time in one than the other. In other words, the prey capture success of predators would have to be equalized within each habitat; strongly density-dependent reproduction within each habitat may be another way to equilibrate the number of offspring produced by each habitat (e.g Levene 1953). Because we are considering a microhabitat scale of variation without barriers to movement by males and predators, there is unlikely to be separate population regulation in each habitat and selection across habitats will be the more appropriate way of modeling natural selection for most organisms.

In developing the model, we made two simplifying assumptions that should nevertheless be biologically realistic. The first is that the visual systems of predators and females are assumed to be similar; that is, the background effects are similar whether viewed by females or by predators so that one male color is always most conspicuous in a particular habitat and vice versa. Conspicuousness to females is often related to conspicuousness to predators (Anderson 1994; Zuk and Kolluru 1998). We also evaluated the hypothesis that the environment did not affect natural selection but did influence sexual selection by having predators select prey at random while females choose mates in a habitat dependent manner. In removing natural selection but keeping female preferences habitat specific, we are essentially following the assumptions of a private communication channel that allows males to transmit signals to females in a way that cannot be perceived by predators (Cummings et al. 2003). In this scenario, we found a stable polymorphism could be maintained over a range of parameter space. Finally, we briefly considered the extreme case of predators and females preferring different morphs within a habitat (i.e. females favor blue males in one habitat, while predators

preferentially prey on yellow males in the same habitat). In this situation, we still found that a stable polymorphism could result, although the conditions are slightly numerically different than when females and predators find the same males to be conspicuous. As most empirical studies show that females prefer conspicuous males that are also most prone to predation (Anderson 1994; Zuk and Kolluru 1998), it is unlikely that the reverse case is commonly seen in nature.

We further assume that neither males nor females choose their habitat but instead move between microhabitats at random. If there were habitat choice, this could change the outcome of the model, as it has been found that habitat matching will broaden the conditions leading to a stable polymorphism (e.g. Maynard Smith 1966; Ravigné et al. 2004). Some empirical evidence suggests that males can select microhabitats. Specifically, males can maximize their conspicuousness while courting females and minimize their conspicuousness at all other times by choosing the appropriate light environments within their habitat (Endler 1991; Endler and Thery 1996). The effectiveness with which males and females choose habitats, however, is unclear. Future research on habitat choice may yield important insights on conditions that will lead to polymorphism maintenance or sympatric speciation.

The basic environmental conditions assumed by our model are common in nature. Fine-scale variation in the sensory environment can be seen in both aquatic and terrestrial environments. In aquatic environments, microhabitats with different visual properties could result from different water depths (Johnsen 2002; Maan et al. 2006), substrate types (Endler 1980), amount and type of overhanging vegetation, or even time of day (Gamble et al. 2003; Johnsen 2002; Endler 1993). Water depth may be a particularly important

way in which habitats can be partitioned, as the properties of visual light change rapidly with changing depth. In fact, the visual systems of many fish species are tuned to the specific light environment of their habitat (Loew and Lythgoe 1978). This match between the sensory system and the environment can even be seen at the microhabitat scale among closely related species with different foraging habitats (Cummings and Partridge 2001). In terrestrial environments, microhabitats with variation in visual properties could occur in places such as forest edges where there are differences in light profiles and substrate (Endler 1993).

Although we have framed our discussion of this model in terms of visual signals that result in selection on body color, the model we present is very general in nature and should be equally applicable to habitat heterogeneity that affects the reception of multiple kinds of signals potentially including sound, chemical, electrical and even tactile. Future empirical studies may add to our understanding of microhabitat variation and its effects by looking carefully at the scale of environmental variation, the frequency distribution of habitat types, and the degree of symmetry in selection between microhabitats. Also, experiments that manipulate microhabitat type, scale, and frequency in replicate populations and then track MCP evolution (similar to Endler's classic work on the evolution of guppy color patterns under different selection regimes, Endler 1980) are necessary to determine the exact role of the environment in MCP maintenance.

The role of the sensory environment in maintaining polymorphism is becoming recognized as increasingly important in part because male color polymorphisms may be a precursor to sympatric speciation (Seehausen et al. 1999; Allender et al. 2003). For example, female choice for conspicuous males in a heterogeneous visual environment has

been proposed as a mechanism for the rapid diversification of cichlid fishes (Seehausen et al. 1997; Allender et al. 2003; Maan et al. 2006). If different sensory environments allow the maintenance of variation in male color, it is possible that divergence could occur if female preferences were also allowed to evolve. Sympatric speciation could result if genes for increasingly strong female preferences spread in the population; this will be explored in future models.

In addition to its theoretical importance, understanding the maintenance of MCPs also has practical relevance because anthropogenic change is rapidly altering the signaling environment of many organisms. If changes in the environment negatively affect discrimination of visual signals, the conditions for the maintenance of male color polymorphisms will be greatly reduced and male color polymorphisms may even collapse. For example, cichlid fish diversity may be threatened because of increasing turbidity, caused by human environmental changes, that obscures male color (Seehausen et al. 1997; Seehausen 2006). Similarly, in terrestrial environments any disturbance to forest structure can have a profound impact on the light regime in the forest, which may once again affect visual displays and thereby disturb mating behavior and reproduction (Endler and Thery 1996).

Sexual selection is increasingly being recognized as an important factor in maintaining genetic and phenotypic diversity, and our model reinforces that idea. Also, many sexually selected traits exhibit an extreme degree of continuous variation. This variation is often attributed to the condition dependence of the traits. Although we model discrete traits here, this work opens up the possibility that the variation in some continuous male traits may also result in part from trade-offs in conspicuousness in

heterogeneous environments. More empirical data on preference strengths, selection from predation, and the effects of microhabitat variation on these processes will lead to a greater ability to predict the environmental and biological conditions that allow polymorphism maintenance and perhaps those that ultimately make sympatric speciation possible.

ACKNOWLEDGEMENTS

The authors would like to thank H. Olofsson, S. Diamond, C. Ledon-Rettig, G. Ragland, J. Knies, A. Rice, M. Ferris, T. Hansen, and two anonymous reviewers for comments on the manuscript, and S. Gray, N. Hamele, N. Frey, M. Whitlock, and J. Greene for helpful discussions. M. Whitlock proposed biological situations under which hard vs. soft selection is appropriate for sexual selection. This work was supported by the National Science Foundation Award DEB-0234849 and DEB-0614166 to MRS, and a National Science Foundation REU grant to UW-Whitewater. The concept for this paper was proposed by JSM, model development and analyses were carried out by AJC and MRS, and all authors contributed to writing.

LITERATURE CITED

Allender, C. J., O. Seehausen, M. E. Knight, G. F. Turner, and N. Maclean. 2003. Divergent selection during speciation of Lake Malawi cichlid fishes inferred from parallel radiations in nuptial coloration. Proc. Natl. Acad. Sci. USA 100:14074-14079.

Anderson, M. 1994. Sexual selection. Princeton University Press, Princeton.

Baer, C. F., M. Dantzker, and M. J. Ryan. 1995. A test for preference of association in color polymorphic poeciliid fish: laboratory study. Enviro. Biol. Fishes 43: 207-212.

Barlow, G. W. 1973. Competition between color morphs of the polychromatic midas cichlid *Cichlosoma citrinellum*. Science 179:806-807.

Boughman, J. W. 2002. How sensory drive can promote speciation. Trends Ecol. Evol. 17:571-577.

Bradbury, J. W. and S. L. Vehrencamp. 1998. Principles of Animal Communication. Sinauer, Sunderland, MA.

Chiao, C.-C., M. Vorobyev, T. W. Cronin, and D. Osorio. 2000. Spectral tuning of dichromats to natural scenes. Vision Res. 40: 3257-2371.

Christiansen, F. B. 1975. Sufficient conditions for protected polymorphism in a subdivided population. Am. Nat. 109:11-16.

Cummings, M. E. and J. C. Partridge. 2001. Visual pigments and optical habitats of surfperch (Embiotocidae) in the California kelp forest. J. Comp. Physiol. A 187: 875-889.

Cummings, M. E., G. Rosenthal, and M. J. Ryan. 2003. A private ultraviolet channel in visual communication. Proc. R. Soc. Lond. B. 270:897-904

de Meeûs, T., Y. Michalakis, F. Renaud, and I. Olivieri. 1993. Polymorphism in heterogeneous environments, evolution of habitat selection and sympatric speciation: soft and hard selection models. Evol. Ecol. 7:175-198.

Dempster, E. R. 1955. Maintenance of heterogeneity. Cold Spring Harb. Symp. Quant. Biol. Sci. 20:25-32.

Eakley, A.L. and A. E. Houde. 2004. Possible role of female discrimination against 'redundant' males in the evolution of colour pattern polymorphism in guppies. Proc. R. Soc. Lond. B. 271:S299-S301.

Endler, J. A. 1980. Natural selection on color patter in poeciliid fishes. Evolution 34:76-91.

---. 1991. Variation in the appearance of guppy patterns to guppies and their predators under different visual conditions. Vision Res. 31:587-608.

---. 1993. The color of light in forests and its implications. Ecol. Monogr. 63:1-27.

Endler J. A. and P. Mielke. 2005. Comparing entire colour patterns as birds see them. Biol. J. Linn. Soc. 86:405-431.

Endler, J. A., and M. Thery. 1996. Interacting effects of lek placement, display behavior, ambient light, and color patterns in three Neotropical forest dwelling birds. Am. Nat. 148:421-452.

Ford, E. B., 1965. Genetic Polymorphism. M.I.T. Press, Cambridge, MA.

Fuller, R. C. and J. Travis. 2004. Genetics, lighting environment, and heritable responses to lighting environment affect male color morph expression in bluefin killifish, *Lucania goodei.* Evolution 58: 1086-1098.

Fuller, R. C., K. L. Carleton, J. M. Fadool, T. C. Spady, and J. Travis. 2005. Genetic and environmental variation in the visual properties of bluefin killifish *Lucania goodei*. J. Evol. Biol. 18:516-523.

Futuyma, D. 1997. Evolutionary Biology 3rd Ed. Sinauer Associates. Sunderland, MA.

Gamble, S., A. K. Lindholm, J. A. Endler, and R. Brooks. 2003. Environmental variation and the maintenance of polymorphism: the effect of ambient light spectrum on mating behaviour and sexual selection in guppies. Ecol. Lett. 6:463-472.

Gliddon, C. and C. Strobeck. 1975. Necessary and sufficient conditions for multiple-niche polymorphisms in haploids. Am. Nat. 109:233-235.

Gray, S. M. and J. S. McKinnon 2006. A comparative description of mating behaviour in the endemic telmatherinid fishes of Sulawesi's Malili Lakes. Enviro. Biol. Fishes 75:471-482.

Gray, S. M. and J. S. McKinnon. 2007. Linking color polymorphism maintenance and speciation. Trends Ecol. Evol. 22: 71-79

Hoffman, E. A. and M. S. Blouin. 2000. A review of colour and pattern polymorphisms in anurans. Biol. J. Linn. Soc. 70:633-665.

Hughes, K. A., L. Du, F. H. Rodd, and D. N. Reznick. 1999. Familiarity leads to female mate preference for novel males in the guppy, *Poecilia reticulata*. Anim. Behav. 58:907-916.

Johnsen, S. 2002. Cryptic and conspicuous coloration in the pelagic environment. Proc. R. Soc. Lond. B. 269:242-256.

Karlin, S., and R. B. Campbell. 1981. The existence of a protected polymorphism under conditions of soft as opposed to hard selection in a multideme population system. Am. Nat. 117:262-275.

Kingston, J. J., G. G. Rosenthal, and M. J. Ryan. 2003. The role of sexual selection in maintaining a color polymorphism in the pygmy swordtail, *Xiphophorus pygmaeus*. Anim. Behav. 65:735-743.

Kirkpatrick, M. 1982. Sexual selection and the evolution of female choice. Evolution 36:1-12.

Kokko, H., M. D. Jennions, and A. Houde. Evolution of frequency-dependent mate choice: keeping up with fashion trends. Proc. R. Soc. Lond. B. 274: 1317-1324.

Levene, H. 1953. Genetic equilibrium when more than one ecological niche is available. Am. Nat. 87:331-333.

Loew, E. R. and J. N. Lythgoe. 1978. The ecology of cone pigments in teleost fishes. Vision Res. 18: 715-722.

Maan, M. E., K. D. Hofker, J. J. M. van Alphen, and O. Seehausen. 2006. Sensory drive in cichlid speciation. Am. Nat. 167:947-954.

Maynard Smith, J. 1966. Sympatric speciation. Am. Nat. 100:637-650.

Olendorf, R., F. H. Rodd, D. Punzalan, A. E. Houde, C. Hurt, D. N. Reznick, and K. A. Hughes. 2006. Frequency-dependent survival in natural guppy populations. Nature 441: 633-636.

Ravigné V., I. Olivieri, U. Dieckmann. 2004. Implications of habitat choice for protected polymorphisms. Evol. Ecol. Res. 6:125-145.

Roulin, A. 2004. The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. Biol. Rev. 79:815-848.

Seehausen, O. 2006. Conservation: Losing biodiversity by reverse speciation. Current Biol. 16: R334-R337.

Seehausen, O., and D. Schluter. 2004. Male-male competition and nuptial-color displacement as a diversifying force in Lake Victoria cichlid fishes. Proc. R. Soc. Lond. B. 271:1345-1353.

Seehausen, O., J. J. M. van Alphen, and F. White. 1997. Cichild fish diversity threatened by eutrophication that curbs sexual selection. Science 277:1808-1811.

Seehausen, O., P. J. Mayhew, and J. J. M. Van Alphen. 1999. Evolution of colour patterns in East African cichlid fish. J. Evol. Biol. 12: 514-534.

Sinervo, B. and C. M. Lively. 1996. The rock-paper-scissors game and the evolution of alternative male strategies. Nature 380: 240-243.

Sinervo, B. and K. R. Zamudio. 2001. The evolution of alternative reproductive strategies: fitness differential, heritability, and genetic correlation between the sexes. J. Heredity 92: 198-205.

Zuk, M., and G. R. Kolluru. 1998. Exploitation of sexual signals by predators and parasitoids. Q. Rev. Biol. 73:415-430.

TABLES

Table 1. Mating Table – Within habitat mate choice. Frequencies of matings involving blue and yellow male morphs in two different habitats when females choose males from within one habitat. Females either carry a blue allele or a yellow allele, and they can be found either in a habitat where blue is conspicuous (H_b, occurring with frequency h_b) or a habitat where yellow is conspicuous (H_y, occurring with frequency $h_{y)}$. Males are either blue or yellow in body color, and again they can be found in either habitat H_b or habitat H_y. Females carrying the blue allele occur with frequency p_b, while blue males occur with frequency of p_b^*. Because males and females move between habitats at random and mating is influenced by habitat, the frequency of each type of mated pair is weighted by the proportion of each type of habitat. Blue males are favored by females in habitat H_b with a preference strength of a_b, while yellow males are favored in habitat H_y by a preference strength of a_y. Matings are normalized so that both types of females have equal mating success, and mating success is not affected by the habitat in which a female mates.

			Males			
			Blue morph		Yellow morph	
			Habitat H_b	Habitat H_y	Habitat H_b	Habitat H_y
Females	carry blue allele	Habitat H_b	$\frac{p_b p_b^* h_b a_b}{z}$	0	$\frac{p_b p_y^* h_b}{z}$	0
		Habitat H_y	0	$\frac{p_b p_b^* h_y}{v}$	0	$\frac{p_b p_y^* h_y a_y}{v}$
	carry yellow allele	Habitat H_b	$\frac{p_y p_b^* h_b a_b}{z}$	0	$\frac{p_y p_y^* h_b}{z}$	0
		Habitat H_y	0	$\frac{p_y p_b^* h_y}{v}$	0	$\frac{p_y p_y^* h_y a_y}{v}$

$z = p_b^* a_b + p_y^*$

$v = p_b^* + p_y^* a_y$

Table 2. Stability regions for asymmetrical parameter combinations. We present parameter values and outcomes for five different selection scenarios. The range of preference strength for yellow males (a_y) required for each possible outcome (blue morph lost, polymorphism, or blue morph fixed) is shown for each combination of parameters. N/A indicates that no biologically realistic value of preference strength (i.e. $a_y > 0$) will result in a stable equilibrium for that outcome. All other findings from other combinations of parameter values were consistent with the results presented.

Parameters				Stability			
h_y	s_b	s_y	a_b	0 (blue lost)	Polymorphism	1 (blue fixed)	Notes
.1	.5	.3	2	N/A	$a_y > 1.17$	$a_y < 1.17$	
.1	.1	.9	1.1	$a_y > 10$	$1.82 < a_y < 10$	$a_y < 1.82$	
.1	.9	.1	1.1	$a_y > .024$	$0 < a_y < .024$	N/A	
.4	.8	.9	3	N/A	$a_y > 1.53$	$a_y < 1.53$	
.4	-.8	-.9	3	N/A	$a_y > 2.22$	$a_y < 2.22$	Natural and sexual selection both favor the same morph

Table 3. Mating Table – Across habitat mate choice. The table shows frequencies of matings involving blue and yellow male morphs in two different habitats when females select males after viewing potential mates from both habitats before mating. Females either carry a blue allele or a yellow allele, while males are either blue or yellow in body color. Both sexes are found in either habitat H_b or habitat H_y. Blue males are favored by females in habitat H_b with a preference strength of a_b, while yellow males are favored in habitat H_y by a preference strength of a_y. Matings are normalized so that both types of females have equal mating success.

		Males	
		Blue Morph	Yellow Morph
Females	carry blue allele	$\frac{p_b p_b^* h_b a_b + p_b p_b^* h_y}{z}$	$\frac{p_b p_y^* h_b + p_b p_y^* h_y a_y}{z}$
	carry yellow allele	$\frac{p_y p_b^* h_b a_b + p_y p_b^* h_y}{z}$	$\frac{p_y p_y^* h_b + p_y p_y^* h_y a_y}{z}$

$$z = p_b^* h_b a_b + p_b^* h_y + p_y^* h_b + p_y^* h_y a_y$$

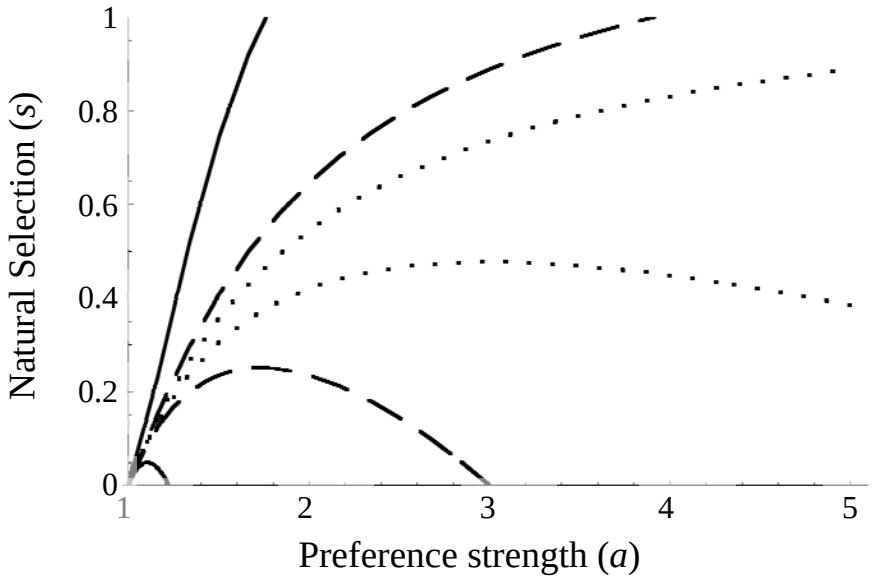

Figure 1. Regions of stability of the polymorphic equilibrium for three values of h_y assuming natural and sexual selection are symmetrical for blue and yellow morphs ($s_b = s_y$ and $a_b = a_y = a$). The area in between each set of patterned lines is the parameter space over which the polymorphic equilibrium is stable for each specific value of h_y (.1, .25, and .45). Dotted lines represent $h_y = .1$, dashed lines represent $h_y = .25$, and solid lines represent $h_y = .45$.

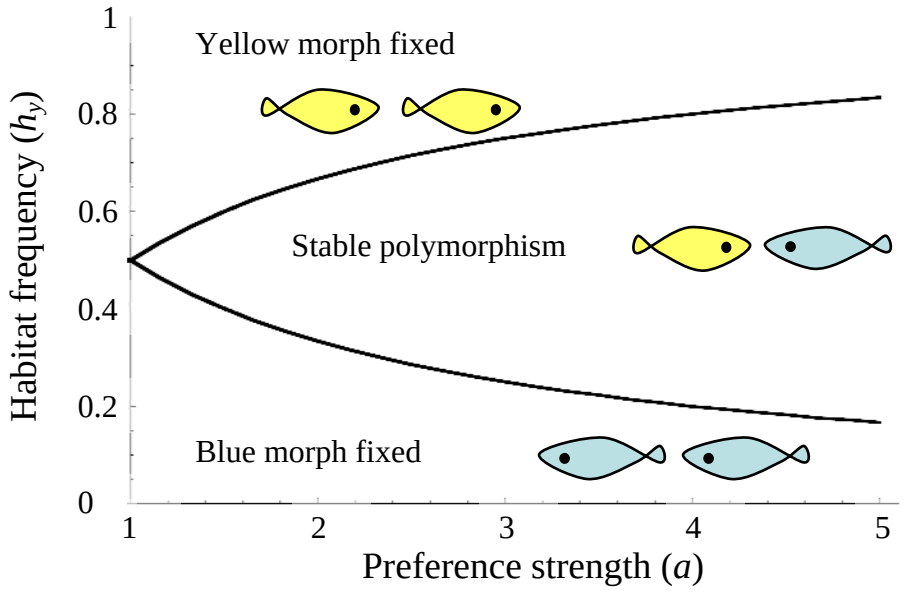

Figure 2a. The region of stability of the polymorphic equilibrium when female preferences are symmetrical and natural selection is removed from the model ($a_b = a_y = a$, $s_b = s_y = 0$). Stronger female preferences allow a polymorphism to be maintained under a wider degree of habitat asymmetry. When a polymorphism cannot be maintained, the fixed morph is dependent on the direction of habitat skew.

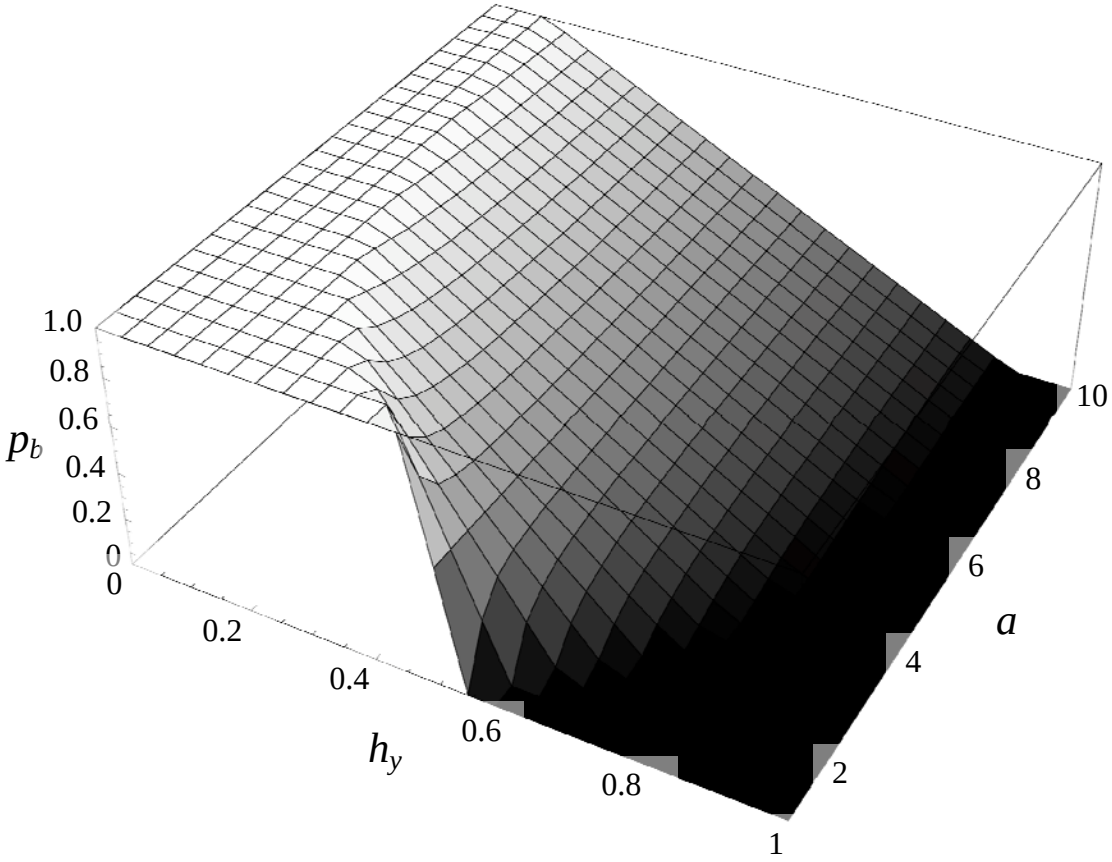

Figure 2b. The frequency of the blue morph at different strengths of female preference (a) and habitat frequency (h_y) when natural selection is removed ($s_b = s_y = 0$) and sexual selection is symmetrical between habitats ($a_b = a_y = a$). White represents fixation of the blue morph while black represents loss.

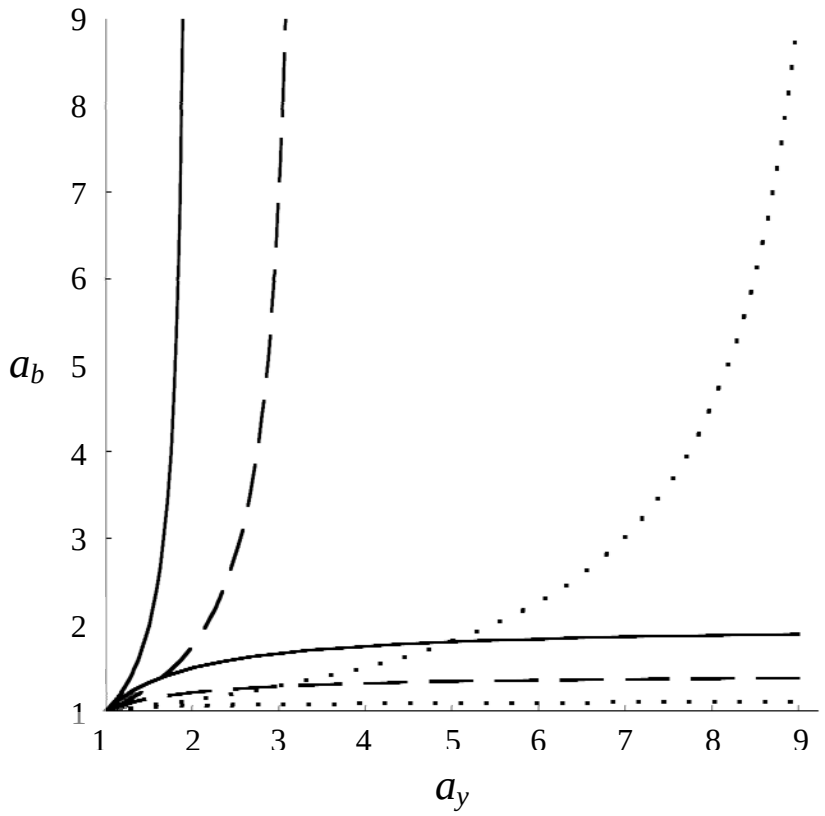

Figure 2c. The strength of female preference that will maintain a color polymorphism when natural selection is not acting ($s_b = s_y = 0$) for three different ratios of habitat frequency. Dotted lines represent $h_y = .1$, dashed lines represent $h_y = .3$, and solid lines represent $h_y = .5$. A polymorphism is maintained in the region between each set of boundary lines and lost with either the blue or yellow morph becoming fixed in the regions outside the boundary lines (blue fixes in the region to the left of the vertical boundary line, and yellow is fixed in the region below the horizontal boundary line). The preference strength needed to maintain a polymorphism increases as habitat frequencies are more strongly skewed.

CHAPTER III

EXTINCTION VIA ADAPTIVE MATE CHOICE: ECOLOGICAL AND EVOLUTIONARY IMPLICATIONS

Abstract - Mate choice is a potent evolutionary force that contributes to the evolution and diversification of striking sexual signals aimed at enhancing attraction and mating success. That the evolution of such traits may have negative consequences for population growth and ultimately contribute to population extinction is a fundamental paradox that has received relatively little attention in the fields of either evolution or ecology. Here, I review some of the ecological and evolutionary implications of extinction that results from adaptive mate choice. I first describe the conditions under which extinction via adaptive processes is most likely. I then discuss the ecological and evolutionary implications that arise when populations undergoing divergent patterns of sexual selection concomitantly experience differential vulnerability to extinction. Generally, evaluating the role of adaptive evolution in extinction is important for understanding how ecological and evolutionary processes impact one another, and for clarifying how different levels of selection (e.g., individual-level selection vs. species selection) interact.

1. INTRODUCTION

Selection promotes the evolution of traits that enhance individual fitness. Yet, populations may experience greater risk of extinction when the evolution of traits that confer high relative fitness to individuals simultaneously reduces population reproductive

rates or population size (a process known variously as “evolutionary suicide”; “Darwinian extinction”; “evolution to extinction”; and “self-extinction”; Matsuda and Abrams 1994a; Dieckmann et al. 1995; Ferrière 2000; Gyllenberg et al. 2002; Houle & Kondrashov 2002; Kokko & Brooks 2003; Webb 2003; Dieckmann & Ferrière 2004; Rankin & López-Sepulcre 2005). That such adaptive evolution could in turn increase a population’s likelihood of extinction is a fundamental paradox of evolution that has received relatively little attention (but see Ferrière 2000; Gyllenberg & Parvinen 2001; Gyllenberg et al. 2002; Fiegna & Velicer 2003; Kokko & Brooks 2003; Webb 2003; Parvinen 2005; Rankin & López-Sepulcre 2005).

Darwin (1871) first recognized that adaptive evolution could result in extinction when he suggested that female preferences could favor traits that were deleterious for both individual male survival and population persistence. Subsequently, Haldane (1932, p. 65) suggested of adaptations in response to competition: “the results may be biologically advantageous for the individual, but ultimately disastrous for the species.” Although counterintuitive, adaptive evolution can lead to extinction when individuals with high relative, but low absolute, fitness spread in a population (Matsuda & Abrams 1994a; Webb 2003; Dieckmann & Ferriére 2004). Traits that convey higher relative fitness can result in reduced population growth and/or smaller population sizes that place the population at higher risk of extinction owing to stochastic events. Alternatively, populations with reduced absolute fitness may be more vulnerable to extinction driven by other species in the environment such as competitors, predators, or pathogens. Similarly, populations that are small and slow growing may be less able to adapt to changing environments (Willi et al. 2006). Thus, any traits that confer higher relative individual

fitness, but that depress a population's ability to persist in the face of deleterious biotic or abiotic circumstances, ultimately may cause a population to go extinct.

Previous work on understanding how adaptation contributes to extinction has focused on the role of resource competition (Haldane 1932; Matsuda & Abrams 1994a; Gyllenberg & Parvinen 2001) or predator-prey dynamics (Rosenzweig 1973; Matsuda & Abrams 1994b; Webb 2003) in promoting extinction. Yet, another key process by which adaptive evolution may ultimately contribute to extinction is sexual selection (Darwin 1871; Houle & Kondrashov 2002; Kokko & Brooks 2003). Indeed, sexual selection is generally stronger than viability selection (Hoekstra et al. 2001; Kingsolver et al. 2001; Kingsolver & Pfennig 2007), and therefore could critically affect both the evolution of traits that enhance mating success, as well as population persistence.

Mate choice in particular is a key force of sexual selection (reviewed in Andersson 1994). Yet how mate choice affects population fitness, growth, and persistence remains unclear. For example, mate choice generally drives the evolution of traits that simultaneously enhance relative reproductive success while diminishing survival (Andersson 1994; e.g. Ryan et al. 1982; Promislow et al. 1994; Gray & Cade 1999). Such a tradeoff between survivorship and mating success can lead to the spread of traits that ultimately reduce population growth and enhance a population's likelihood of extinction (Darwin 1871; Kokko & Brooks 2003). Alternatively, female preference for elaborate traits that indicate male condition can lead to enhanced fertility rates and increased offspring survival and growth (reviewed in Andersson 1994). Indeed, such condition-dependent mate choice could foster rapid adaptation and contribute to the

maintenance of population size and reproductive rates that actually buffer populations from extinction (Lorch et al. 2003; Pfennig & Pfennig 2005).

Whether female mate choice therefore enhances – or reduces – a population's risk of extinction depends on the costs of elaborate signals, the benefits of mate choice, and their effects on population fitness. Yet, we know relatively little of the conditions under which mate choice will tend to increase a population's risk of extinction. We also do not fully understand how the particular traits that females use in mate choice contribute to population extinction risk. Addressing these problems is important, because extinction – and its causes – underlie patterns of ecological and evolutionary diversity.

Here, my goals are twofold. First, I suggest when adaptive mate choice is likely to contribute to a population's risk of extinction. In particular, I focus on how evolutionary tradeoffs in mate choice decisions can generate different levels of extinction risk among populations that differ in how those trade-offs are resolved. Moreover, I discuss how the targets of mate choice – along with their underlying developmental and genetic architecture – place populations at greater risk of extinction. Second, I evaluate the evolutionary and ecological consequences of differential extinction risk between populations. As I suggest below, evaluating the role of adaptive mate choice in population-level extinction is important for understanding species ranges, species richness, community diversity, and macorevolutionary patterns of trait evolution and diversification.

2. ADAPTIVE MATE CHOICE AND THE CAUSES OF EXTINCTION RISK

Mate choice can contribute to population extinction risk in at least two non-mutually exclusive ways. First, population extinction risk can be affected by the way in which females benefit from their mating decisions. In particular, how females negotiate the cost-benefit tradeoffs of mating decisions may play a critical role in affecting a population's risk of extinction. Second, the particular traits that females use to choose mates can dictate whether mate choice is likely to increase a population's extinction risk. I discuss each of these routes to extinction below.

Mate choice trade-offs and extinction risk

Females often face tradeoffs when selecting a mate in that they face both costs and benefits of their mate choice decisions (e.g. females may pay energetic costs or risk predation to search for a preferred mate). Such tradeoffs arise from environmental factors such as predators, pathogens, or competitors, which limit or alter the nature of female mate choice in some populations versus others. How females negotiate tradeoffs imposed by these factors can reduce absolute population fitness and therefore increase the probability of population extinction. Moreover, because these factors often vary among populations, how female mate choice varies in response to these factors can generate population differences in risk of extinction.

One factor that generates trade-offs in mate choice is predation. Females are often at increased risk of predation while searching for a mate or when associating with preferred, but conspicuous, males (reviewed in Magnhagen 1991). In high-predation populations, therefore, females face a tradeoff between the costs and benefits of mating with a preferred male, which females from low-predation populations do not face. These

trade-offs can be apparent in differences in the degree of choosiness of females in high versus those in low predation environments. For example, in guppies, females from high-predation populations reduce their level of sexual activity and their choosiness in the presence of predators, while females from low-predation populations show no differences in behavior between the presence and absence of a predator (Godin & Briggs 1996). Generally, if the costs of decreased choosiness are manifest in decreased offspring fitness or decreased rates of reproduction, populations with more predators may be smaller, slower growing, and less adaptable (sensu Lorch et al. 2003). Such populations would thus face a higher risk of extinction compared to populations without predators.

A second characteristic of the environment that can have profound effects on female mate choice is the presence or absence of parasites and pathogens. Many pathogen species can be transmitted socially or sexually, and avoiding diseased males may be a major driver in the evolution of female preferences (Hamilton & Zuk 1982; see also Zuk 1992 and references therein). Generally, parasite mediated female choice will likely enhance population fitness and buffer populations from extinction, especially if pathogens have large negative effects on population dynamics.

When pathogens are transmitted socially or sexually, however, preferred males may in some cases have higher parasite loads than non-preferred males (Merilä & Sheldon 1999; Pfennig & Tinsley 2002). This could occur if preferred males have more mates and thus have a greater probability of contracting, and then spreading, socially or sexually transmitted parasites than non-preferred males. When attractive males harbor the highest disease load, this can leave choosy females more vulnerable to parasites than indiscriminate females. Thus, females in highly parasitized populations face a tradeoff

not experienced by females in low parasite populations; that is, attractive males may confer fitness benefits to the female or her offspring, but also may lead to the female becoming parasitized herself (Able 1996). Females that risk infection by mating with high quality males may therefore produce more or better quality offspring, but such choice behavior may foster the spread of parasites in the population that ultimately reduces population viability.

A third factor that can generate tradeoffs for females is the presence of heterospecifics. If heterospecifics resemble high-quality conspecifics, females may tradeoff the benefits they would receive from mating with the most attractive mates to ensure mating with conspecifics (Higgie & Blows 2008; Pfennig 1998, 2000, 2008). For example, in Mexican spadefoot toads (*Spea multiplicata*), the calls of high quality males resemble those of a heterospecific species, Plains spadefoot toads (*S. bombifrons*) (Pfennig 2000). In sympatric populations, *S. multiplicata* females favor calls resembling those of average males, while in allopatric populations, females prefer more extreme calls resembling those of *S. bombifrons* (Pfennig 2000). Here, sympatric females give up the advantages of mate quality, presumably to guarantee species identity (Pfennig 2000). In particular, by mating with average males rather than extreme males, females sacrifice fertilization success and offspring quality (Pfennig 2000, 2008). This could translate into a lower net reproductive rate and thus a decrease in mean population fitness in populations with competitors compared to those without competitors (Pfennig & Pfennig 2005).

In the discussion above, female choice is adaptive at the level of the individual, but at the population level, mean population fitness, and potentially, population viability,

may be reduced because of the costs of mate choice in certain environments. Moreover, because environments are variable, populations will experience differential risk of extinction depending on how mate choice varies in response to the environment. Thus, the impact of the environment on mate choice behavior affects both the potential for adaptive mate choice to contribute to extinction and the likelihood that populations will experience different risks of extinction.

Targets of mate choice that increase extinction risk

The way in which females tradeoff the fitness consequences of mate choice can affect a population's risk of extinction. Additionally, the specific traits targeted by females and the underlying genetic and developmental architecture of those traits may be important in determining whether adaptive mate choice enhances a population's risk of extinction. Below, I discuss four different ways in which the types of traits and the mechanisms of trait production might affect extinction risk.

First, whether the traits under sexual selection reinforce or oppose the direction of natural selection may have key consequences for a population's risk of extinction. If sexual and natural selection are in opposition, then the likelihood of extinction may be higher than when mate choice favors a trait that is advantageous under viability selection. For example, females often prefer conspicuously colored males (reviewed in Andersson 1994); however, conspicuous coloration often results in increased predation risk (Andersson 1994; Zuk & Kolluru 1998; Husak et al. 2006). That is, brightly colored males that attract females also attract predators, which could reduce mean population fitness and thereby decrease population viability.

Second, extravagant traits may be more developmentally costly to produce and maintain, and their expression may come at the cost of developing other organ systems (Nijhout & Emlen 1998; Emlen 2001). In horned beetles, for example, the production by males of an extravagant signal – a large thoracic horn – comes at the expense of copulatory organ size and even testes mass (Simmons & Emlen 2006; Parzer & Moczek 2008). Skimping on these latter traits may reduce population fertility rates and thereby reduce population size. Consequently, populations with more severe tradeoffs between the expression of secondary sexual traits and other organ systems may be at higher risk of extinction than those facing less severe trade-offs.

Third, the genetic architecture underlying a male trait may make extinction more likely in some populations versus others. Both antagonistic pleiotropy and linkage disequilibrium can lead to negative genetic correlations between attractiveness and viability (Brooks 2000). In guppies, male attractiveness shows a negative genetic correlation with offspring survival (Brooks 2000). The putative explanation for this is that many of the genes for ornamentation in guppies are located on the Y chromosome near a region with suppressed recombination. This reduced recombination could lead to the accumulation of deleterious mutations on the Y chromosome (Brooks 2000) that hitchhike along with genes for preferred male traits. Again, females preferring attractive males may have increased attractiveness in male offspring, but at a cost of an accumulation of deleterious mutations in the population that makes the population less viable.

Intralocus sexual conflict (i.e. when genes have different fitness consequences in males and females) may also lead to increased probability of extinction. For example, in

Drosophila, reproductive success shows a negative genetic correlation between the sexes (Chippindale et al. 2001), which may lead to different fitness consequences for the sons and daughters of females who mate with a preferred male (Chippindale et al. 2001). Side-blotched lizards face a similar conflict, where large males produce sons with a higher viability, while small males father daughters with a higher viability (Calsbeek & Sinervo 2004; see also Calsbeek & Bonneaud (2008) for an example of a similar phenomenon in *Anolis* lizards). Thus, females must tradeoff the fitness of male and female offspring based on a preferred mate. Unless females can mitigate this cost through biasing offspring sex ratio (Calsbeek & Sinervo 2004), a tradeoff between son and daughter fitness could result in decreased mean population fitness. Such decreased population fitness could arise if adaptive evolution of males and females is constrained or if reproduction and survivorship are reduced. Consequently, decreased mean population fitness could, in turn, result in higher vulnerability to extinction.

Fourth, at the species level, the genetic system of sex determination may play a role in vulnerability to extinction via mate choice by affecting the strength of sexual selection. Theoretical work and a meta-analysis of empirical data by Reeve and Pfennig (2003) suggested that taxonomic biases in species with elaborate male secondary sexual characters might be a result of the genetic system. Specifically, the model they developed showed that a rare allele encoding either a male ornament or a female preference for that ornament is less likely to be lost due to drift in species with male homogamety (ZZ/ZW or ZZ/ZO) than in species with male heterogamety (XX/XY or XX/XO). Consistent with this prediction, a comparative analysis among different taxa revealed that sexual selection was stronger in systems with male homogemety (Reeve & Pfennig 2003).

This taxonomic bias in the strength of sexual selection may lead to biases in extinction risk, and may explain patterns in empirical work comparing strength of sexual selection with extinction risk. Morrow & Pitcher (2003) found that, in birds, threatened species were under stronger sexual selection pressure than non-threatened species on average, whereas in mammals, there was no relationship between the strength of sexual selection and extinction risk (Morrow & Fricke 2004). While both studies used morphology as an indicator of the strength of sexual selection rather than measuring selection directly, this difference in findings may in part be due to the different genetic systems (i.e. males are homogametic in birds, and heterogametic in mammals) between these classes. Although suggestive, additional comparative studies are required to determine how chromosomal sex determination mediates extinction risk through its effects on mate choice.

Vulnerability to extinction via adaptive female mate choice is complex. The environmental conditions under which mate choice occurs and the targets of mate choice will contribute to extinction risk. Both empirical and theoretical work is badly needed to evaluate the effects of mate choice on population dynamics and persistence. Such studies are important, because extinction affects both ecological and evolutionary patterns of diversity. Below, I discuss some of the ecological and evolutionary consequences of extinction via adaptive mate choice.

3. ECOLOGICAL IMPLICATIONS

Differential vulnerability to extinction can have potentially important ecological consequences that are rarely considered. As I describe below, differential extinction can

affect ecological patterns and processes including range limits, species richness, and community dynamics. Indeed, because understanding how mate choice may limit population growth and size can help explain patterns of biodiversity, it can have important implications for conservation.

Range size is an important component of species-level extinction risk (Manne et al. 1999; Purvis et al. 2000), and population-level extinction risk may dictate species ranges. Recent studies suggest that mate choice may limit the size of species ranges by affecting population viability. In ground hoppers (*Tetrix spp*.), for example, two species (*T. ceperoi* and *T. subulata*) have similar habitat ranges and habitat preferences; however, they rarely co-occur at the same site (Hochkirch et al. 2007). Laboratory and field studies have shown that the reproduction of *Tetrix ceperoi*, is severely reduced in the presence of *T. subulata* because *T. ceperoi* males preferentially court *T. subulata* females. In contrast, the reverse pattern does not occur. Hochkirch et al. (2007) suggest that this reproductive interference has lead to 'sexual exclusion' and likely explains the lack of coexistence in these species. Here, male *T. ceperoi*'s preferences for *T. subulata* females reduces the fitness of both males and females, and could increase the probability of extinction for this species, which is currently listed as endangered (Hochkirch et al. 2007). Competitive exclusion for resources has had obvious and strong affects on species distributions (Gause 1934; Hardin 1960; Connell 1961), and similar patterns seem likely for sexual exclusion (Groning & Hochkirch 2008). This work has interesting implications for the driving forces of community composition, and more work on 'sexual exclusion' is clearly needed.

If mate choice leads to reduced ranges, this can, in turn, increase the probability of species extinction. Generally, species with broader geographic ranges are less likely to go extinct (Jablonski 1986). Presumably, having a broader range renders a species less vulnerable to chance events or to the negative consequences of habitat loss in one part of its range. As I describe in more detail below, such species level consequences of range size have important implications for understanding macroevolutionary patterns of diversity.

Community composition may also be influenced by differential extinction driven by adaptive mate choice. That is, the species richness and abundance of a community may be shaped, in part, by the strength of sexual selection in the component species. In a study of North American bird communities, for example, Doherty et al. (2003) found that dichromatic species had a much higher local extinction rate than monochromatic birds (plumage color was used as an indicator of the strength of sexual selection). However, they also found that rates of species turnover were higher for dichromatic species as well, which more than compensated for the higher local extinctions rates (Doherty et al. 2003). That is, sexually dimorphic species, while more likely to go extinct, were also more likely to re-colonize an area after an extinction event. Therefore, while species under strong sexual selection may face higher extinction risk at a local scale, other life history characteristics may ameliorate this risk at a global scale. Thus, mate choice can therefore impact community composition, without necessarily altering species richness, over time. Nevertheless, further studies are needed to ascertain the relationship between mate choice and community composition and richness.

Although many studies have considered how mate choice can affect the evolution of traits, few studies have considered the ecological implications of mate choice. As mate choice likely has strong effects on ecological patterns and processes, more studies are needed to specifically elucidate how mate choice may affect population density, effective population size, range limits, and species richness.

4. EVOLUTIONARY IMPLICATIONS

As I describe above, the nature of adaptive mate choice can have critical consequences for population dynamics and persistence. Over longer time scales, population extinction via adaptive mate choice may have evolutionary implications that extend far beyond selection on male traits and female preferences. Furthermore, differential extinction of species can explain macroevolutionary patterns of diversity in terms of both numbers of species and the diversity (or lack thereof) of sexual traits among those groups. In this section, I highlight how differences in extinction patterns contribute to these outcomes.

Mate choice may have evolutionary implications that reach beyond the evolution of male traits and female preferences. That extravagant male traits may attract predators or have other viability costs has been recognized since Darwin (1871). Less apparently, traits that seem adaptive over short time scales may increase species extinction risk over longer time scales. For example, many studies have shown that females often prefer large male body size (Andersson 1994). In general, larger individuals have increased survival, fecundity, and mating success (Kingsolver & Pfennig 2007). This selection on body size can explain Cope's Rule, that is, the tendency for species within a lineage to increase in

size over evolutionary time (Cope 1896; Kingsolver & Pfennig 2004). Because of the benefits of size, preferences for large body size will often be adaptive for individuals, and populations where these preferences can be expressed may be buffered from extinction over microevolutionary time scales compared to populations where mate choice for large size is precluded (e.g. Pfennig 2000).

The outcome of selection, however, may differ depending on the time scale being considered. While large size is adaptive over short time scales, it can also render a population more vulnerable to extinction over geological time scales. Because species with larger body sizes generally also have life history characteristics that leave them more vulnerable to extinction during periods of environmental change, these species may be more likely to go extinct over macroevolutionary time than their smaller counterparts (Bonner 1988; Kingsolver & Pfennig 2007). Therefore, although unintuitive, it may be that mate choice behaviors that are adaptive over shorter, microevolutionary time scales may actually increase the probability of extinction over longer, macroevolutionary time scales. Moreover, if the extinction events that selectively crop the larger species occur very infrequently (e.g., millions of years between events), then it is highly unlikely that individual-level selection will occur favoring other traits in such individuals that decrease their extinction risk.

Differential extinction via adaptive mate choice can also lead to species level selection. That is, selection at the individual level can result in differential survival of species with traits rendering them less susceptible to extinction (Webb 2003). In predator-prey models, Rosenzweig (1973) showed species level selection should favor prudent predators, as the evolution of increased attack rates often led to extinction.

Similarly, species level selection might affect patterns observed in female mate choice. That is, when individual level selection favors mate choice strategies that increase the risk of population extinction, species with those traits should be disfavored over evolutionary time. Such a process could cause species with certain mate choice strategies that increase extinction risk to disappear at faster rates and more frequently than those that lack these strategies. For example, strictly Fisherian patterns of mate choice that might be likely to contribute to extinction risk (Kokko & Brooks 2002) would become less common than condition-dependent mate choice, which may buffer populations from extinction (Lorch et al. 2003). Over time, the characteristics of species might change, just as the characteristics of individuals might changes within a population. In other words, species level selection may make certain make choice patterns predominate relative to others in a given taxonomic group.

Finally, differential risk of extinction via mate choice may account for differences in species richness among taxonomic groups. Sexual selection is generally expected to drive speciation, and taxonomic groups that experience strong sexual selection are expected to be more species rich (reviewed in Ritchie 2007). Yet, comparative studies provide only mixed support for this prediction. One explanation is that species undergoing certain forms of sexual selection may also be more likely to go extinct. Thus, sexual selection may contribute to higher rates of speciation, but these higher rates of species production are counter-balanced by higher extinction rates (Doherty et al. 2003; Morrow et al. 2003; Ritchie 2007). A better understanding of the interplay between sexual selection and extinction risk may help explain sexual selection's role in generating

– and maintaining – species richness and macroevolutionary patterns of diversity, such as why some taxonomic groups are more diverse than others.

5. CONCLUSIONS

A handful of tantalizing examples of adaptation towards extinction in nature and in the lab have emerged recently (reviewed in Rankin & López-Sepulcre 2005). However, the conditions under which adaptive mate choice can lead to extinction are still poorly understood, and both theoretical and empirical studies are needed to elucidate the specific mechanisms by which extinction can occur as a result of adaptive mate choice.

Evaluating the effects of mate choice on population level features such as population growth, population size, and the maintenance of genetic variation that contributes to adaptability in changing circumstances is a critical first step in assessing the role of mate choice in extinction risk. By doing so, we will gain needed insight into behavior's role in population dynamics. Perhaps more importantly, establishing whether a link exists between mate choice and population processes will lend greater insight into the role of individual behavior in shaping community dynamics, species distributions, and macroevolutionary patterns of trait evolution and biodiversity.

We are grateful to David Pfennig, Jonathan Rowell, Amber Rice, Ryan Martin, Sumit Dhole, Elizabeth Wojtowicz, Maria Servedio, and Joel Kingsolver for helpful discussion and comments that improved the manuscript. This work was supported by grants from the National Science Foundation and the National Institutes of Health to KP.

REFERENCES

Able, D. J. 1996. The contagion indicator hypothesis for parasite-mediated sexual selection. *Proc. Natl. Acad. Sci. USA* **93**, 2229-2233.

Andersson, M. 1994 *Sexual selection*. Princeton, NJ: Princeton University Press.

Bonner, J. T. 1988 *The evolution of complexity by means of natural selection*. Princeton, NJ: Princeton University Press.

Brooks, R. 2000 Negative genetic correlation between male sexual attractiveness and survival. *Nature* **406**, 67-70.

Calsbeek, R. & Bonneaud, C. 2008 Postcopulatory fertilization bias as a form of cryptic sexual selection. *Evolution* **62**, 1137-1148.

Calsbeek, R. & Sinervo, B. 2004 Within-clutch variation in offspring sex determined by differences in sire body size: cryptic mate choice in the wild. *J. Evol. Biol.* **17**, 464-470.

Chippindale, A. K., Gibson, J. R. & Rice, W. R. 2001 Negative genetic correlation for adult fitness between sexes reveals ontogenetic conflict in *Drosophila*. *Proc. Natl. Acad. Sci. USA* **98**, 1671-1675.

Connell, J. H. 1961 The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* **42**, 710-723.

Cope, E. D. 1896 *The primary factors of organic evolution*. Chicago, IL: Open Court Publishing.

Darwin, C. 1871 *The descent of man, and selection in relation to sex*.London, UK: John Murry.

Dieckmann, U. & Ferrière, R. 2004 Adaptive dynamics and evolving biodiversity. In *Evolutionary Conservation Biology* (eds R. Ferrière, U. Dieckmann, & D. Couvet), pp. 188-224. Cambridge, UK: Cambridge University Press.

Dieckmann, U., Marrow, P. & Law, R. 1995 Evolutionary cycling in predator-prey interactions: population dynamics and the red queen. *J. Theor. Biol.* **176**, 91-102.

Doherty, P. F. Jr., Sorci G., Royle, J. A., Hines, J. E., Nichols, J. D. & Boulinier T. 2003 Sexual selection affects local extinction and turnover in bird communities. *Proc. Natl. Acad. Sci. USA* **100**, 5858-5862.

Emlen, D. J. 2001 Costs and the diversification of exaggerated animal structures. *Science* **291,**1534-1536.

Ferrière, R. 2000 Adaptive responses to environmental threats: evolutionary suicide, insurance, and rescue. Options, Laxenburg, Austria: IIASA, 12-16.

Fiegna, F. & Velicer G. J. 2003 Competitive fates of bacterial social parasites: Persistence and self-induced extinction of *Myxococcus xanthus* cheaters. *Proc. R. Soc. B* **270**, 1527-1534.

Gause, G. F. 1934 *The struggle for existence*. Baltimore, MD: Williams and Wilkins.

Godin, J.-G. & Briggs, S. E. 1996 Female mate choice under predation risk in the guppy. *Anim. Behav.* **51**, 117-130.

Gray, D. A. & Cade, W. H. 1999 Sex, death and genetic variation: Natural and sexual selection of cricket song. *Proc. R. Soc. B* **266**, 707-709.

Groning, J. & Hochkirch, A. 2008. Reproductive interference between animal species. *Q. Rev. Biol*. **83**, 257-282.

Gyllenberg, M. & Parvinen, K. 2001 Necessary and sufficient conditions for evolutionary suicide. *Bull. Math. Biol.* **63**, 981-993.

Gyllenberg, M., Parvinen, K. & Dieckmann, U. 2002 Evolutionary suicide and evolution of dispersal in structured metapopulations. *J. Math. Biol.* **45**, 79-105.

Haldane, J. B. S. 1932 *The causes of evolution*. Princeton, NJ: Princeton University Press.

Hamilton, W. D. & Zuk, M. 1982 Heritable true fitness and bright birds - a role for parasites. *Science* **218**, 384-387.

Hardin, G. 1960 The competitive exclusion principle. *Science **131***, 1292-1297.

Higgie, M. & Blows, M. W. 2008 The evolution of reproductive character displacement conflicts with how sexual selection operates within a species. *Evolution* **62**, 1192-1203.

Hochkirch, A., Gröning, J. & Bücker, A. 2007 Sympatry with the devil: Reproductive interference could hamper species coexistence. *J. Anim. Ecol.* **76**, 633-642.

Hoekstra, H. E., Hoekstra, J. M., Berrigan, D., Vignieri, S. N., Hoang, A., Hill, C. E., Beerli, P. & Kingsolver, J. G. 2001 Strength and tempo of directional selection in the wild. *Proc. Natl. Acad. Sci. USA* **98**, 9157-9160.

Houle, D. & Kondrashov, A. S. 2002 Coevolution of costly mate choice and condition-dependent display of good genes. *Proc. R. Soc. B* **269**, 97-104.

Husak, J. F., Macedonia, J. M., Fox, S. F. & Sauceda, R. C. 2006 Predation cost of

conspicuous male coloration in collared lizards (*Crotaphytus collaris*): An experimental test using clay-covered model lizards. *Ethology* **112**, 572-580.

Jablonski, D. 1986 Background and mass extinctions - the alternation of macroevolutionary regimes. *Science* **231,** 129-133.

Kingsolver, J. G. & Pfennig, D. W. 2004 Individual-level selection as a cause of Cope's rule of phyletic size increase. *Evolution* **58**, 1608-1612.

Kingsolver, J. G. & Pfennig, D. W. 2007 Patterns and power of phenotypic selection in nature. *BioScience* **57**, 561-572.

Kingsolver, J. G., Hoekstra H. E., Hoekstra, J. M., Berrigan, D., Vignieri, S. N., Hill, C. E., Hoang, A., Gibert, P. & Beerli, P. 2001 The strength of phenotypic selection in natural populations. *Am. Nat.* **157**, 245-261.

Kokko, H. & Brooks, R. 2003 Sexy to die for? Sexual selection and the risk of extinction. *Ann. Zool. Fennici* **40**, 207-219.

Lorch, P. D., Proulx, S., Rowe, L. & Day, T. 2003 Condition-dependent sexual selection can accelerate adaptation. *Evol. Ecol. Res.* **5**, 867-881.

Magnhagen, C. 1991 Predation risk as a cost of reproduction. *Trends Ecol. Evol*. **6**, 183-186.

Manne, L. L., Brooks, T. M. & Pimm, S. L. 1999 Relative risk of extinction of passerine birds on continents and islands. *Nature* **399**, 258-261.

Matsuda, H. & Abrams, P. A. 1994a Runaway evolution to self-extinction under asymmetrical competition. *Evolution* **48**, 1764-1772.

Matsuda. H. & Abrams, P. A. 1994b Timid consumers: self-extinction due to adaptive change in foraging and anti-predator effort. *Theor. Popul. Biol.* **45**: 76-91.

Merilä, J. & Sheldon, B. C. 1999 Testis size variation in the greenfinch *Carduelis chloris*: relevance for some recent models of sexual selection. *Behav. Ecol. Sociobio.* **45**, 115-123.

Morrow, E. H. & Fricke, C. 2004 Sexual selection and the risk of extinction in mammals. *Proc. R. Soc. B* **271**, 2395-2401.

Morrow, E. H. & Pitcher, T. E. 2003 Sexual selection and the risk of extinction in birds. *Proc. R. Soc. B* **270**, 1793-1799.

Morrow, E. H., Pitcher, T. E. & Arnqvist, G. 2003 No evidence that sexual selection is an 'engine of speciation' in birds. *Ecol. Lett.* **6**, 228-234.

Nijhout, H. F. & Emlen, D. J. 1998 Competition among body parts in the development and evolution of insect morphology. *Proc. Natl. Acad. Sci. USA* **95**, 3685-3689.

Parvinen, K. 2005 Evolutionary suicide. *Acta Biotheoretica* **53**, 241-264.

Parzer, H. F. & Moczek, A. P. 2008 Rapid antagonistic coevolution between primary and secondary sexual characters in horned beetles. *Evolution* **62,** 2423-2428.

Pfennig, K. S. 1998 The evolution of mate choice and the potential for conflict between species and mate-quality recognition. *Proc. R. Soc. B* **265,** 1743-1748.

—. 2000 Female spadefoot toads compromise on mate quality to ensure conspecific matings. *Behav. Ecol.* **11**, 220-227.

—. 2008 Population differences in condition-dependent sexual selection may promote divergence in non-sexual traits. *Evol. Ecol. Res.* **10,** 763-773.

Pfennig, K. S. & Pfennig, D. W. 2005 Character displacement as the "best of a bad situation": Fitness trade-offs resulting from selection to minimize resource and mate competition. *Evolution* **59**, 2200-2208.

Pfennig, K. S. & Tinsley, R. C. 2002 Different mate preferences by parasitized and unparasitized females potentially reduces sexual selection. *J. Evol. Biol*. **15**, 399-406.

Promislow, D., Montgomerie, R. & Martin, T. E. 1994 Sexual selection and survival in North American waterfowl. *Evolution* **48**, 2045-2050.

Purvis, A., Gittleman, J. L., Cowlishaw, G. & Mace, G. M. 2000 Predicting extinction risk in declining species. *Proc. R. Soc. B* **267**, 1947-1952.

Rankin, D. J. & López-Sepulcre, A. 2005 Can adaptation lead to extinction? *Oikos* **111**, 616-619.

Reeve, H. K. & Pfennig, D. W. 2003 Genetic biases for showy males: Are some genetic systems especially conducive to sexual selection? *Proc. Natl. Acad. Sci. USA* **100**, 1089-1094.

Ritchie, M. G. 2007 Sexual selection and speciation. *Annu. Rev. Ecol. Evol. Syst.* 38, 79-102.

Rosenzweig, M. L. 1973 Evolution of the predator isocline. *Evolution* **27**, 84-94.

Ryan, M. J., Tuttle, M. D. & Rand, A. S. 1982. Bat predation and sexual advertisement in a Neotropical Anuran. *Am. Nat.* **119**, 136-139.

Simmons, L. W. & Emlen, D. J. 2006 Evolutionary trade-off between weapons and testes. *Proc. Natl. Acad. Sci. USA* **103**, 16346-16351.

Webb, C. 2003 A complete classification of Darwinian extinction in ecological interactions. *Am. Nat.* **161**, 181-205.

Willi, Y., Van Buskirk, J. & Hoffmann, A. A. 2006 Limits to the adaptive potential of small populations. *Annu. Rev. Ecol. Evol. Syst*. **37**, 433-458.

Zuk, M. 1992 The role of parasites in sexual selection - current evidence and future directions. *Adv. Study Behav.* **21**, 39-68.

Zuk, M. & Kolluru, G. R. 1998 Exploitation of sexual signals by predators and parasitoids. *Q. Rev. Biol*. **73**, 415-430.

CHAPTER IV

COMPARING RANGES: USING HISTORIC DATA TO TEST HYPOTHESES ABOUT RANGE EXPANSION

Abstract - As both global warming and the rate of species invasions intensify, understanding the dynamics of how ranges change through time will be of critical importance. Furthermore, as ranges determine species interactions, a spatially explicit approach towards examining ranges can have not only practical implications, but can be useful in studying evolutionary history. One often underutilized source of information on historic range dynamics are museums and other natural history collections. Here, I use museum records to look at the ranges of two species of spadefoot toads over recent history. I attempt to address two questions: 1) How have ranges changed over time? and 2) How has habitat occupancy changed in one section of the range? Although there have been dramatic changes to the landscape in which these two species live over the last 100 years due to the intensification of agriculture, collection records did not show a strong signature of either range expansion or changes in habitat occupancy. However, variation in collection effort over time is a confounding variable that is difficult to tease apart from changes in ranges or occupancy. Thus, although museum records remain an immensely valuable resource for both ecological and evolutionary studies, documenting the dramatic changes to the habitat that are currently underway will require more rigorous and detailed record keeping than in the past.

INTRODUCTION

As species ranges are shifting increasingly rapidly due to accidental and deliberate introductions (Rhymer and Simberloff 1996), land-use change (Pimm and Raven 2000; Yamaura et al. 2009), and global climate change (Walther et al. 2002; Parmesan and Yohe 2003), understanding range dynamics is becoming increasingly important. Indeed, given the conservation threats imposed by anthropogenic change, an accurate evaluation of how ranges shift over time is vital.

While much work has focused on predicting novel distributional changes that will result under future climate change scenarios (Hole et al. 2009; Jetz et al. 2007) and on evaluating recent phenological changes within a range (Miller-Rushing and Primack 2008; Cleland et al. 2007), less work has focused on how historic anthropogenic change may have previously affected species distributions. Although humans have been facilitating range changes for millennia (e.g. Case and Bolger 1991; Gippoliti and Amori 2006), the rate of human facilitated range shifts has increased dramatically. Documenting the anthropogenic impact on ranges in recent history can be useful for both examining the impact of anthropogenic change on a population and for predicting future range changes.

A potentially valuable resource in documenting recent range changes are spatially and temporally explicit records from museums and natural history collections. These collections provide a wealth of direct information about where species have been found in the recent past (Graham et al. 2004). This resource, though often underutilized by evolutionary biologists, can provide a host of data to explicitly test both ecological and evolutionary hypotheses about range dynamics (Graham et al. 2004).

Studying range dynamics can provide information both about the ecology and the evolution of a species in several ways. First, selection pressures differ between range edge and range cores, resulting in potential differences between individuals in these populations (Kirkpatrick and Barton 1997). Observed evolutionary differences between edge and core populations include morphology (e.g. Phillips et al. 2006) and behavior (e.g. Duckworth and Badyaev 2007). Also, because of the nature of core vs. edge populations, we expect to see differences between these two habitats in terms of population dynamics. Specifically, species tend to be more abundant and more continuously distributed at the center of the range, and rarer and more patchily distributed at the periphery of the range (Brown 1984; Lawton 1993).

Understanding range dynamics can also be important in understanding species interactions. When a species moves into a new area, novel species interactions can result (Williams and Jackson 2007), potentially leading to extinction (Parker and Gilbert 2004) or hybridization (Mooney and Cleland 2001; Rhymer and Simberloff 1996). This is an increasing issue as climate change is differentially affecting rates of movement for interacting species (reviewed in Parmesan 2006). Furthermore, across the distribution of interacting species, we may expect to see different outcomes of species interactions depending on whether one or both species are at the center or edge of their range, or if populations differ in the length of their interactions over evolutionary time.

To get a complete picture of range dynamics, it is important to consider both shifts in range boundaries and in habitat occupancy within the range. First, range boundaries can change as populations move from the edge of the previous range into novel areas. Such is the case with species moving up latitude because of rising

temperatures (Parmesan and Yohe 2003). At a smaller scale, populations within the boundaries of the range may still undergo distributional changes if individuals move into novel habitats or into newly created habitats. Both processes can occur either because of an evolutionary change allowing a population to survive in a novel habitat (e.g. mine tailing adapted plants, Antonovics 1972) or if the habitat itself changes in such a way that it becomes suitable (e.g. shifts in altitude due to climate change, Walther et al. 2002).

Here, I use museum records to evaluate the recent distribution of two species of spadefoot toads, *Spea bombifrons* and *S. multiplicata* in the US southwest, specifically in southern Arizona and New Mexico. This area of the country has undergone immense changes to the landscape due to anthropogenic affects over the last 100 years that could potentially affect amphibian communities in the region. The goal here was to determine whether museum specimens could be used to address two specific questions: 1) Are there difference in when each of these two species were first collected in the southwest? and 2) Are there differences in habitat occupancy between these species in the southwest? Below, I describe the study system used to address these questions.

MATERIALS AND METHODS

Study System

Two species of spadefoot toads, the Plains spadefoot (*Spea bombifrons*) and the Mexican spadefoot (*S. multiplicata*), co-occur over a large region in the American southwest (Stebbins 2003). Both species spend most of their lives underground, emerging only during the summer rainy season to feed and breed. Breeding is explosive and occurs in ephemeral pools that form after monsoon rains (Bragg 1965). When both species

attend the same breeding aggregation, hybridization can occur (Simovich 1985; Pfennig and Simovich 2002).

Both *S. bombifrons* and *S. multiplicata* develop rapidly (indeed, members of the genus *Spea* are among the fastest developing amphibians (Bragg 1967)). *S. bombifrons*, however, takes significantly longer to complete metamorphosis (27 days on average) than *S. multiplicata* (24 days on average) (Pfennig and Simovich 2002). As pond duration is typically very short, ponds routinely dry before tadpoles complete metamorphosis (Pfennig 1992). Rapid development time is thus highly advantageous in these environments, and the different development times for *S. bombifrons* and *S. multiplicata* suggest that *S. multiplicata* may persist in habitats in which *S. bombifrons* can not.

While most of the range of *S. bombifrons* falls within the Great Plains, a habitat defined by fairly flat topography and prairie grassland, the southwestern edge of the range is more arid (USEPA 2003). This area has also undergone tremendous land-use changes due to the introduction of the rail system and the intensification of agriculture by the end of the 19th century. The introduction of cattle ranching in the late 1800's (Gehlbach 1981; Bock and Bock 2000) may have had a particularly strong effect on the amphibian communities in this area, as natural ephemeral pools are routinely deepened by ranchers to provide a longer lasting water source for their cattle. Indeed, today, these 'cattle tanks' provide the primary breeding habitat for both *Spea spp*. (pers. obs).

Agriculture can affect species distributions in two general ways. First, changes to the habitat can either allow species to invade new areas or to be excluded from previously occupied areas. Both would affect the overall range of the species. Second, agriculture could lead to increases or decreases in abundance within the habitat depending on

whether habitat changes are favorable or deleterious to the species. While this would not change the overall range of the species, it can affect species interactions, and potentially shift a source population to a sink population or vice versa.

In *Spea spp.*, I expect that agriculture could differentially affect each species, as the San Simon valley represents the edge of the range for *S. bombifrons*, and the range core for *S. multiplicata* (Stebbins 2003). For *S. bombifrons*, the creation of longer lasting breeding ponds via cattle ranching may have potentially allowed the slower developing species to expand into a habitat that would otherwise be too arid for their survival. Alternatively, if *S. bombifrons* was historically present in the area, but in more mesic habitats such as riverbeds, the creation of longer lasting breeding ponds could result in increasing abundance and habitat occupancy in the region. Ranching could have less of an effect on *S. multiplicata*, as this species should be more established in the region.

Here, I made use of historic museum collections to document current and historic ranges of both species of sapdefoot toads to test the hypothesis that agriculture has differentially impacted these two species in southern Arizona and New Mexico. This work suggests how museum specimens can be used to address both ecological and evolutionary questions.

Museum records

To determine historical ranges of these species, I used collection records for both *S. bombifrons* and *S. multiplicata* from 38 museums throughout the United States and Canada. This resulted in 14,695 total records. The 38 museums chosen were primarily large or historically important government and private collections and those associated

with larger colleges and universities. As smaller collections were excluded, the records included here do not represent every specimen possible, which might potentially affect the exact extent of the geographic range. By focusing on larger collections, though, I were able to get a very large number of records (i.e., 14,695), and finding and georeferencing every available specimen would be prohibitively time consuming. Also, because I obtained such a large number of records from geographically dispersed museums, the exclusion of any possible missed samples from smaller, regional museums did not likely affect the results.

Of the 14,695 records initially obtained, I removed duplicate records, those with incorrect or incomplete locality information, and those missing the year of collection. For the purposes of this study, a record was considered a duplicate if the collector, date of collection, locality of collection, and museum was identical to that of another record from the same museum (i.e., when two individual toads were collected at the same time from the same place and were given different museum accession numbers, only one record was used). As I am interested in evaluating geographic distributions, removing duplicate records leaves the actual number of locations in a region where each species was collected. This left 1,915 *S. bombifrons* and 2,084 *S. multiplicata* unique records ranging in year of collection from 1836 to 2007. Each record was georeferenced and assigned an accuracy code based on the precision of the locality data. These georeferenced points were then plotted by year of collection in ArcView 9.3 (Fig 1).

The majority of collection records, 91.3%, were reasonably precise (i.e. within 10 km). Because of vague locality information, the remaining records were less precise. This was especially problematic for early records – specimens collected before 1930 could

often be identified only to county or potentially even region within a state. Because eliminating imprecise records would lead to a loss of much of the early data on species distributions, the most critical time period of this study, I included records if I could identify the collection location to within 100 miles. Although this has the potential to affect the accuracy of estimates of the distribution of each species, this likely does not alter the overall conclusions of this study for several reasons. First, these records make up a small proportion of the total number of records. Second, the majority of these records are found within the core of the range, and so do not influence estimates of range area. Finally, 70% of the more imprecise records could still be estimated to within at least 30 miles, a fairly good estimate given the ranges of both these species are quite large.

To better visualize collection effort across the entire range for both species, I constructed minimum convex polygons around all records collected within 15 year intervals between 1870 and 2005 (Fig 2). This provided information both on how collection effort has been distributed across space and time and also on known occurrence localities of each species over time.

To evaluate changes in presence and abundance of both species within the San Simon valley, AZ, I selected an area surrounding and extending to the west of San Simon, AZ and I compiled collection records over time for both species within only this region (Fig 3). I chose this specific area for several reasons. First, if agriculture facilitated a range expansion by *S. bombifrons*, this expansion likely proceeded from east to west following the ranching industry and could potentially be detected by focusing just on this more xeric habitat. Second, based on Stebbins (2003), this area represented edge habitat for *S. bombifrons* and more core habitat for *S. mutliplicata*. This makes it a good location

for determining whether these two species were differentially affected by agriculture. Finally, the area I choose lies within the Chihuanhuan Desert and Madrean Archipelago ecoregions. This region is fairly mountainous, and contains primarily shrubs and arid grassland (USEPA 2003). As the habitat is similar throughout this area, I would expect similar processes affecting species distribution and abundance within this region.

Statistical Analysis

To evaluate at collection effort over time, I extracted all the collection records within the San Simon region and compared the number of records collected for each species by year. To do so, I first plotted all the records over time for both species, including only presence records (i.e. if a species was not collected in a year, it did not receive a measure of zero but was simply not included in the analysis). For both *S. bombifrons* and *S. multiplicata,* I fit a linear regression and tested the equality of the slopes for these species within the San Simon valley (Sokal and Rohlf 1995). To better compare the rates of collection between these two species, I also looked at log transformed ($\log_{10}$) cumulative data over time. As early collection records were very infrequent, here I only considered consecutive years over which at least 1 specimen was collected in any 5 year time period. In both analyses, I am assuming that the slope of a linear regression should indicate relative collection effort, with steeper slopes indicating increased collection effort or increasing species abundance (Pyšek and Prach 1993). In comparing the two species, I am assuming that slope represents collection effort for species that are native, and collection effort *plus* the invasion rate for species that are expansive (Crawford and Hoagland 2009). If *S. bombifrons* has recently expanded into

this area while *S. multiplicata* has always been present, I expected the slope for this species to be significantly steeper than that of *S. multiplicata*. Here, the slope should reflect the increasing abundance as *S. bombifrons* expanded into, and became established in, the San Simon region.

RESULTS

Examining the maps of collection records for each species shows a strong effect of time on collection effort, with only very sparse records available before 1900, and good collection effort throughout the geographic extent of the range not occurring till around the 1940's (Fig 2). This is seen in both species, as the geographic extent of collection records increases substantially in each time interval examined until reaching a more stable distribution by the 1940's. After 1974, collections actually decrease in each subsequent time period.

Even with relatively rare records from before the 1940's, though, interesting patterns of species distribution can be observed. Looking in Arizona, which was thought to represent core habitat for *S. mulitplicata* and edge habitat for *S. bombifrons*, only *S. multiplicata* are found prior to 1900. Although there are only a small number of records here compared to later time points, this does indicate that there was collection effort in the area but that *S. bombifrons* was not collected. Over the next two time periods, only two *S. bombifrons* were collected in the state during those 30 years compared to 30 *S. multiplicata* records. By the 1945 time period, *S. bombifrons* is collected fairly commonly in this area, and is actually found further west than indicated by field guide range maps (Stebbins 2003). A similar pattern is seen for *S. mutlipliata* in northern

Texas. Specifically, *S. multiplicata* is not collected at all in this region prior to 1900, and only one record to the east of north Texas is seen by 1915. This species is not well collected in the region until 1945, while *S. bombifrons* was collected far more commonly than *S. multiplicata* in each earlier time period.

When looking specifically within the San Simon region, I find no difference in slope between these two species in the San Simon region when looking at the number of records collected per year (*S. multiplicata*, slope = 0.009, *S. bombifrons*, slope = 0.018, $F_{1, 88} = 0.0489$, p=0.826) (Fig 4). While here I used only presence data (i.e. if a species was not found in a given year, it was not included rather than being assigned a value of 0), this result of no difference in slope between the two species is robust when a lack of collection in a year is assumed to be a true absence (i.e. if one species was found in a year but the other wasn't, the second species was given a value of '0' for that year). This result is also robust when data is subset to include shorter time intervals (e.g. excluding early years for which there is inconsistent collection effort (until 1950) or later years when collection effort levels off (after 1980).

When considering cumulative collection effort, I restricted the analysis to the years 1953-2004, so only consecutive years with at least 1 record in a five year time period were included. Here again I see no difference in slope between these two species (*S. multiplicata*, slope = 0.019, *S. bombifrons*, slope = 0.0213, $F_{1, 100} = 1.0836$, p=0.3004) (Fig 5).

Looking at the data from this region does show that *S. bombifrons* appears in collection records later than *S. multiplicata* by a difference of 16 years (1909 vs. 1893). There are, however, no records of either species in the intervening years, making it

difficult to say whether the later appearance of *S. bombifrons* in collections is due to a later arrival in the area rather than being an artifact of infrequent early collection efforts. Also, *S. bombifrons* is consistently less common than *S. multiplicata* in the region. Across the entire time period (between 1893 and 2004), there were only four years where *S. bombifrons* was collected more frequently than *S. multiplicata.* Even in later years, when collection effort was more consistent and *S. bombifrons* should be better established if it did recently invade the area, I see strong difference in abundance. Looking specifically from 1953-2004 (the years included in the cumulative analysis above), shows that there were only five years from which *S. multiplicata* was not collected vs. 20 years in which *S. bombifrons* was not collected. Given the large time period involved and the multiple collectors who provided this data, this pattern strongly suggests *S. bombifrons* is rarer in the area rather than a bias towards collecting *S. multipicata.*

DISCUSSION

Understanding range dynamics over time has important consequences for evolutionary theory, while also having applications in conservation. Here, I used museum specimens to look at patterns of species occurrences over time for the last 100 years. While interesting patterns emerge in distribution, disentangling biological significance from collection effort can be challenging.

In studying distributional changes over time, there are two important questions to consider: 1) When did a species first arrive in a region, and 2) How does habitat occupancy change over time after a species first arrives? The first question addresses

large scale range expansion, while the second question addresses habitat usage within a region. Both questions can potentially be addressed using information deposited in natural history collection. First, by looking at when a species first appears in a collection, it can be possible to determine at least the latest possible arrival date of a species. Second, looking at the number of unique occurrences of a species within an area can provide valuable information on habitat saturation and potentially abundance. Both methods have been especially useful in tracking range changes in invasive and expansive species (Delisle et al. 2003; Groden et al. 2005; Crawford and Hoagland 2009).

Here, I considered two species of spadefoot toads that may have differentially been affected by agriculture in the US southwest. In this region of the country, the advent of cattle ranching in the late 1800's (Gehlbach 1981; Bock and Bock 2000) altered the natural landscape as ranchers began excavating deep pools to provide water for their cattle. This could have affected distributions in both ways described above. First, by artificially deepening ephemeral ponds, pond duration is extended. This may have allowed *S. bombifrons*, with its longer development time, to expand into this region as suitable breeding areas became increasingly available. Second, the creation of new breeding habitat might have allowed both species to increase in habitat occupancy within the region.

By looking at both the spatial distribution over the entire range of each species, and by looking at the number of unique localities within a region, I wanted to address whether or not one species is a recent arrival in southeastern Arizona, and whether there is evidence of a change in habitat occupancy for either or both species in the region. In looking at collection in southeastern Arizona, I do see that *S. bombifrons* appears in

natural history collections far later than *S. multiplicata* within the San Simon region (Fig 4). This could be due to a true range expansion facilitated by the introduction of cattle ranching to the region. Alternatively, however, it could also be that *S. bombifrons* has always occurred in the region, albeit at lower abundances than *S. multiplicata*. Given that *S. bombifrons* has consistently been collected less frequently than *S. multiplicata* (Fig. 4), it does appear to be the rarer species in this habitat. This could result in a decreased likelihood of being collected, especially in early years when collection efforts were limited, and could thus explain why this species shows up later in collection records.

To determine habitat usage over time, I looked at the number of unique occurrences within the San Simon region (Fig 4). Here, I expected that a relative difference between the number of unique sites from which a species was collected could indicate these species were differentially affected by agriculture. That is, if *S. bombifrons* showed an increase in records over time, relative to *S. multiplicata*, that would indicate the species was moving into and becoming established in the area. Instead, I find that collections for both species remain similar, relative to each other, over time. This could suggest either that both species were not affected by ranching or that they were affected in the same way. If cattle tanks were constructed at natural pond sites, it could be that both species continued to breed in the same areas, and patterns in collection records reflect changes in collection effort with each species being collected in proportion to its relative abundance. Alternatively, if ranchers created new breeding ponds, both species may have moved into the newly available habitat at the same rate. Disentangling these two alternative hypotheses remains difficult given the limits of museum collections

In all studies that make use of museum collections, there are important caveats that must be considered (see Graham et al. 2004 and references therein). Most importantly is that records are usually not the result of a systematic survey, but instead reflect a hodgepodge of specimens from different collectors, each of which had a different motivation for collecting any particular specimen. This results in a strong potential for bias in the numbers of individuals, and the types of specimens, that are collected from any given locality. At the same time, because collecting is done by human beings, accessibility to a site has a strong effect on the likelihood that a geographic area will be collected (Hijmans et al. 2000). Finally, as different collectors and different museums catalog different data with each specimen, utilizing multiple collections can require substantial effort to standardize important data such as locality and date of collection.

By using common species that have been heavily collected throughout their ranges, I have attempted to avoid some of the problems inherent in using rarer or more charismatic species that are less likely to be collected. Indeed, I found a total of over 14,500 records for these species, indicating a strong history of collection effort. Other problems with using museum specimens are, however, unavoidable. A key issue at stake is the differences in the distribution of species in edge vs. core habitats within the range. At the center of a species' range, abundances are expected to be substantially higher that at the range periphery (Brown 1984; Lawton 1993). Just due to this difference in abundance, the likelihood of finding, and then collecting, a specimen should be higher in core vs. edge populations. This is relevant for addressing my initial question of range expansion because, within the San Simon region, *S. multiplicata* has historically been

(Fig 4) and continues to be (pers. obs.) far more common than *S. bombifrons*, making it difficult to distinguish between a recent arrival in this region and low abundance leading to spotty collection records.

Also, with any attempt to use museum records to document the first appearance of a species within a region, it is essential to evaluate the history of collection effort in the same geographic extent by looking at closely related species with similar habitat requirements. Otherwise, it is impossible to disentangle the initial arrival of a species from the initial arrival of collectors in a region. Here, I used two species in part to control for collection effort; however, if one species is substantially more common than the other, and collection effort is sporadic during the time period of interest, as is the case with this study, arguments about first arrival date must be made with caution. For example, in North Texas, *S. multiplicata* appears later and less frequently than *S. bombifrons*, which could be interpreted as evidence for a range expansion. However, it is possible that this simply reflects the lower abundance of this species in this region. At this point, there is no biological evidence suggesting a recent range expansion, so this later explanation seems likely. In the San Simon region, genetic evidence suggests that *S. multiplicata* has been established in the area for substantially longer than *S. bombifrons* (Rice and Pfennig 2008). Although the genetic evidence suggests that S. bombifrons has undergone a range expansion (Rice and Pfennig 2008), the genetic data do not indicate how recently this range expansion may have occurred. In this study, I have documented that *S. bombifrons* was present by 1909; however, the incompleteness of early collection efforts makes it impossible to determine whether this represents a new introduction to the region or if the population was well established but rare at that time.

Determining the true history of distribution for both species in my study has important implications for understanding the history of species interactions between them. Within the San Simon valley, hybridization frequency between *S. multiplicata* and *S. bombifrons* has decreased within 27 years (Pfennig 2003). This decline in hybridization frequency is most likely the result of recent secondary contact. Here, I do see that both species have co-occurred within the San Simon region since at least 1909. It could be that *S. bombifrons* has undergone a recent range expansion prior to 1909. Alternatively, *S. bombifrons* could have historically been present in the area but segregated in habitat use until relatively recently. Unfortunately, museum records are inadequate for distinguishing between these competing hypotheses.

As anthropogenic change is altering species distributions at an increasingly rapid pace, the need to understand the effects of this change on living species is vital. Yet, even with common species such as the spadefoot toads, important and basic questions about their biology remain. Although these species have been heavily collected, the available data are still too sparse to disentangle the effects of landscape change from collection effort. At the same time, we have almost no data on how landscape change has affected the population dynamics of these species either across their range or at the local scale. This study highlights the need for more systematic efforts to document species occurrences. With the advent of more advanced and less expensive GPS technology, efforts by citizen scientists (such as the Audubon Christmas bird counts and the North American Butterfly Association butterfly counts) can provide a wealth of data on species occurrences in both space and time. Ensuring that this data continues to be collected, and

that it is stored in a standardized format that is accessible to scientists, will be vital in providing a better understanding of the many consequences of anthropogenic change.

ACKNOWLEDGEMENTS

I would like to thank Jack Weiss, Allen Hurlbert, and members of the Moody lab, particularly Todd Jobe and Anne Trainor, for advice on statistical analyses. My committee, including David Pfennig, Joel Kingsolver, Maria Servedio, and Aaron Moody provided guidance during the development of this research. Cris Ledón-Rettig, Ryan Martin, Sarah Diamond, and Marty Ferris provided helpful discussions. Sarah Seiter, Elizabeth Wojtowicz, Sumit Dholé, and Laura Exline gave helpful comments on the manuscript. Finally, the multiple museum curators who helped provide me with locality records were absolutely invaluable in the completion of this work, as was the GIS advice of Amanda Henley.

REFERENCES

Antonovics, J. 1972. Population dynamics of *Anthoxanthum odoratum* on a zinc mine. J. Ecol. 60: 351-365.

Blair, W. F. 1974. Character displacement in frogs. Am. Zool. 14: 1119-1125.

Bock, C.E. & Bock, J.H. 2000. The View from Bald Hill: Thirty Years in an Arizona Grassland. University of California Press, Berkeley, CA.

Bragg, A. N. 1965. Gnomes of the night: the spadefoot toads. University of Pennsylvania Press, Philadelphia, Pennsylvania, USA.

Bragg, A. N. 1967. Recent studies on sapdefoot toads. Bios 38: 75-84.

Britch, S. C., M. L. Cain, and D. J. Howard. 2001. Spatio-temporal dynamics of the *Allonemobius fasciatus-A. socius* mosaic hybrid zone: a 14-year perspective. Mol. Ecol. 10:627-638.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. Am. Nat. 124: 255-279.

Case, T. J. and D. T. Bolger. 1991. The role of introduced species in shaping the distribution and abundance of island reptiles. Evol. Ecol. 5, 272-290.

Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, M. D. Schwartz. 2007. Shifting plant phenology in response to global change. Trends Ecol. Evol. 22: 357-365.

Commission for Environmental Cooperation. Unpublished. Ecological Regions of North America. <ftp://ftp.epa.gov/wed/ecoregions/cec_na/>

Coyne, J. A. and Orr, H. A. 2004. *Speciation*. Sinauer Associates.

Crawford, P. H. C. and B. W. Hoagland. 2009. Can herbarium records be used to map alien species invasion and native species expansion over the past 100 years? J. Biogeogr. 36: 651-661.

Delisle, F., C. Lavoire, M. Jean, and D. Lachance. 2003. Reconstructing the spread of invasive plants: taking into account biases associated with herbarium specimens. J. Biogeography 30: 1033-1042.

Dobzhansky, T. 1940. Speciation as a stage in evolutionary diver-gence. Am. Nat. 74:312-321.

Duckworth, R. A. and A. V. Badyaev. 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. PNAS 104: 15017-15022.

Gehlbach, F.R. 1981. Mountain Islands and Desert Seas: A Natural History of the U.S.–Mexico Borderlands. Texas A & M University Press, College Station, TX.

Gippoliti, S. and G. Amori. 2006. Ancient introductions of mammals in the Mediterranean Basin and their implications for conservation. Mammal Rev. 36: 37-48.

Graham, C. H., S. Ferrier, F. Huettman, C. Moritz, and T. Peterson. 2004. New developments in museum-based informatics and applications in biodiversity analysis. Tree 19: 497-503.

Groden, E., F. A. Drummond, J. Garnas, and A. Franceour. 2005. Distribution of an invasive ant, *Myrmica rubra* (Hymenoptera: Formicidae), in Maine. J. Econ. Entomol. 98: 1774-1784.

Hijmans, R. J., K. A. Garrett, Z. Huamán, D. P. Zhang, M. Schreuder, and M. Bonierbale. 2000. Accessing the geographic representativeness of genebank collections: the case of Bolivian wild potatoes. Con. Biol. 14: 1755-1765.

Hole, D. G., S. G. Willis, D. J. Pain, L. D. Fishpool, S. H. M. Butchart, Y. C. Collingham, C. Rahbek, and B. Huntley. 2009. Projected impacts of climate change on a continent-wide protected area network. Ecology Letters 12, 420-431.

Jetz, W., D. S. Wilcove, A. P. Dobson. 2007. Projected impacts of climate and land-use change on the global diversity of birds. Plos Biology 5: 1211-1219.

Jones, J. M. 1973. Effects of thirty years hybridization on the toads *Bufo americanus* and *Bufo woodhousii fowleri* at Bloomington, Indiana. Evolution 27:435-448.

Kirkpatrick, M. and N. H. Barton. 1997. Evolution of a species' range. Am. Nat. 150: 1-23.

Lawton, J. H. 1993. Range, population abundance and conservation. Trends in Ecol. Evol. 8: 409-413.

Miller-Rushing, A. J. and R. B. Primack. 2008. Global warming and flowering time in Thoreau's Concord: A community perspective. Ecology 82: 332-341.

Mooney, H. A. and E. E. Cleland. 2001. The evolutionary impact of invasive species. PNAS 98: 5446-5451.

Parker, I. M. and G. S. Gilbert. 2004. The evolutionary ecology of novel plant-pathogen interactions. Annu. Rev. Ecol. Evol. Systm. 35: 675-700.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Systm. 37: 637-669.

Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37-42.

Pfennig, D. W. 1992. Polyphenism in spadefoot toad tadpoles as a locally adjusted evolutionary stable strategy. Evolution 46: 1408-1420.

Pfennig, K. S. and M. A. Simovich. 2002. Differential selection to avoid hybridization in two toad species. Evolution 56 1840-1848.

Pfennig, K. S. 2003. A test of alternative hypotheses for the evolution or reproductive isolation between spadefoot toads: Support for the reinforcement hypothesis. Evolution 57: 2842-2851.

Pfennig, K. S. 2007. Facultative mate choice drives adaptive hybridization. Science 318: 965-967.

Phillips, B. L., G. P. Brown, J. K. Webb, R. Shine. 2006. Invasion and the evolution of speed in toads. Nature 439: 803.

Pimm, S. L. and P. Raven. 2000. Extinction by numbers. Nature 403: 843-845.

Pyšek, P. and Prach, K. 1993. Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe. J. Biogeography 20: 413-420.

Rhymer, J. A. and Simberloff, D. 1996. Extinction by hybridization and introgression. Annu. Rev. Ecol. Syst. **27**: 83-109.

Rice, A. M. and D. W. Pfennig. 2008. Analysis of range expansion in two species undergoing character displacement: why might invaders generally 'win' during character displacement? J. Evol. Biol. 21: 696-704.

Simovich, M. A. 1985. Analysis of a hybrid zone between the spadefoot taods *Scaphiopus multiplicataus* and *Scaphiopus bombifrons.* Ph.D. diss., University of California, Riverside, CA.

Simovich, M. A., Sassaman, C. A., and Chovnick, A. 1991. Post-mating selection of hybrid toads (*Scaphiopus multiplicatus* and *Scaphiopus bombifrons*). Proc. San Diego Soc. Nat. Hist. 1991: 1-6.

Sokal, R. R. and Rohlf, F. J. 1995. Biometry, 3rd edn. W. H. Freeman and Co., New York.

Stebbins, R. C. 2003. A Field Guide to Western Reptiles and Amphibians: Peterson Field Guides. New York, Houghton Mifflin Company.

U.S. Environmental Protection Agency, 2006, Level III ecoregions of the continental United States (revision of Omernik, 1987): Corvallis, Oregon, USEPA – National Health and Environmental Effects Research Laboratory, Map M-1, various scales.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O., and Bairlein, F. 2002. Ecological responses to recent climate change. Nature 416: 389–395.

Williams, J. W. and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. Front. Ecol. Environ. 5: 475-482.

Yamaura, Y., T. Amano, T. Koizumi, Y. Mitsuda, H. Taki & K. Okabe. 2009 Does land-use change affect biodiversity dynamics at a macroecological scale? A case study of birds over the past 20 years in Japan. Animal Conservation 12: 110-119.

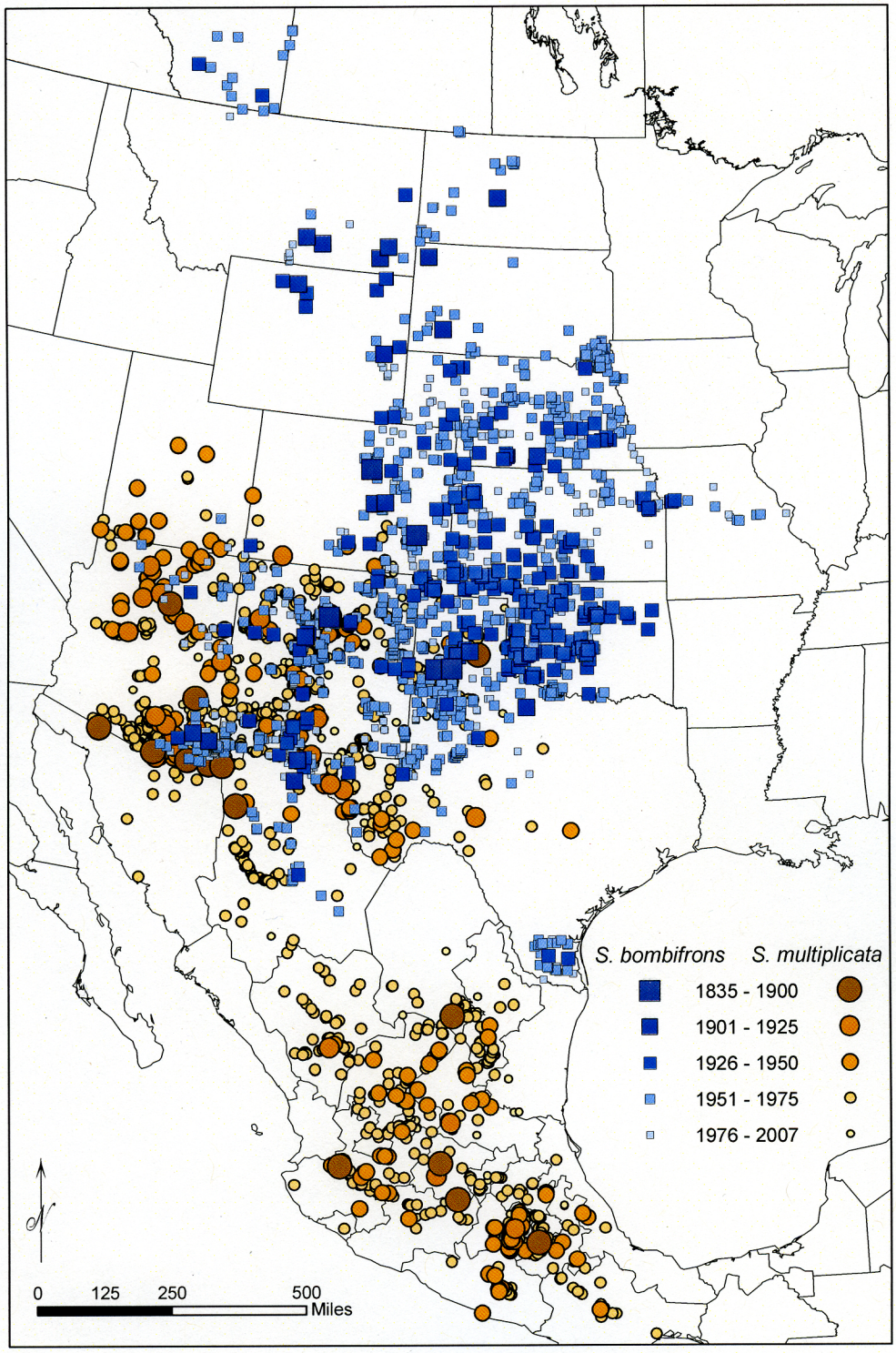

Fig 1. Museum collection records for both *S. bombifrons* and *S. multiplicata*, plotted by year of collection.

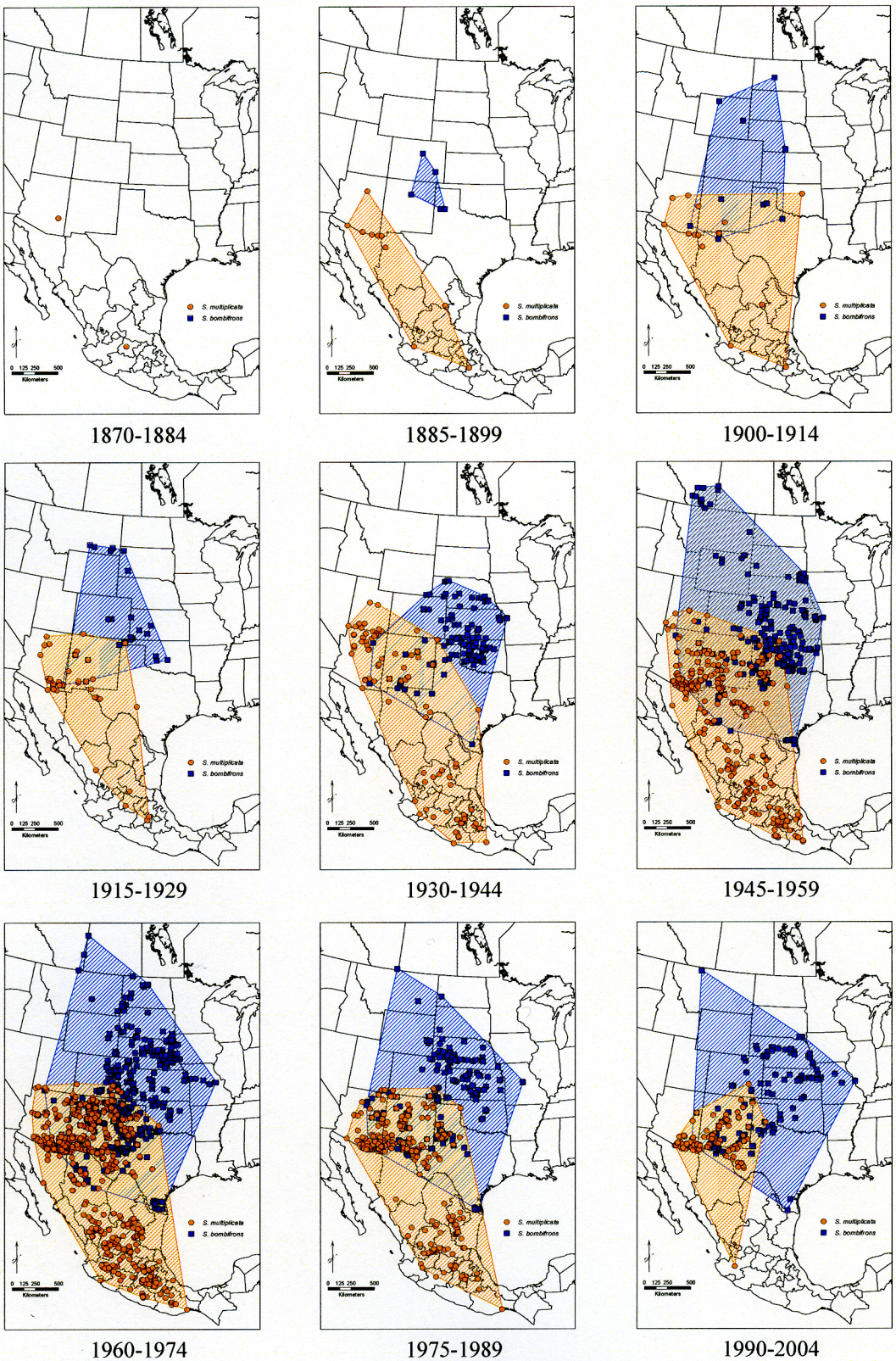

Fig. 2. Collection records over time for both *S. multiplicata* and *S. bombifrons*.

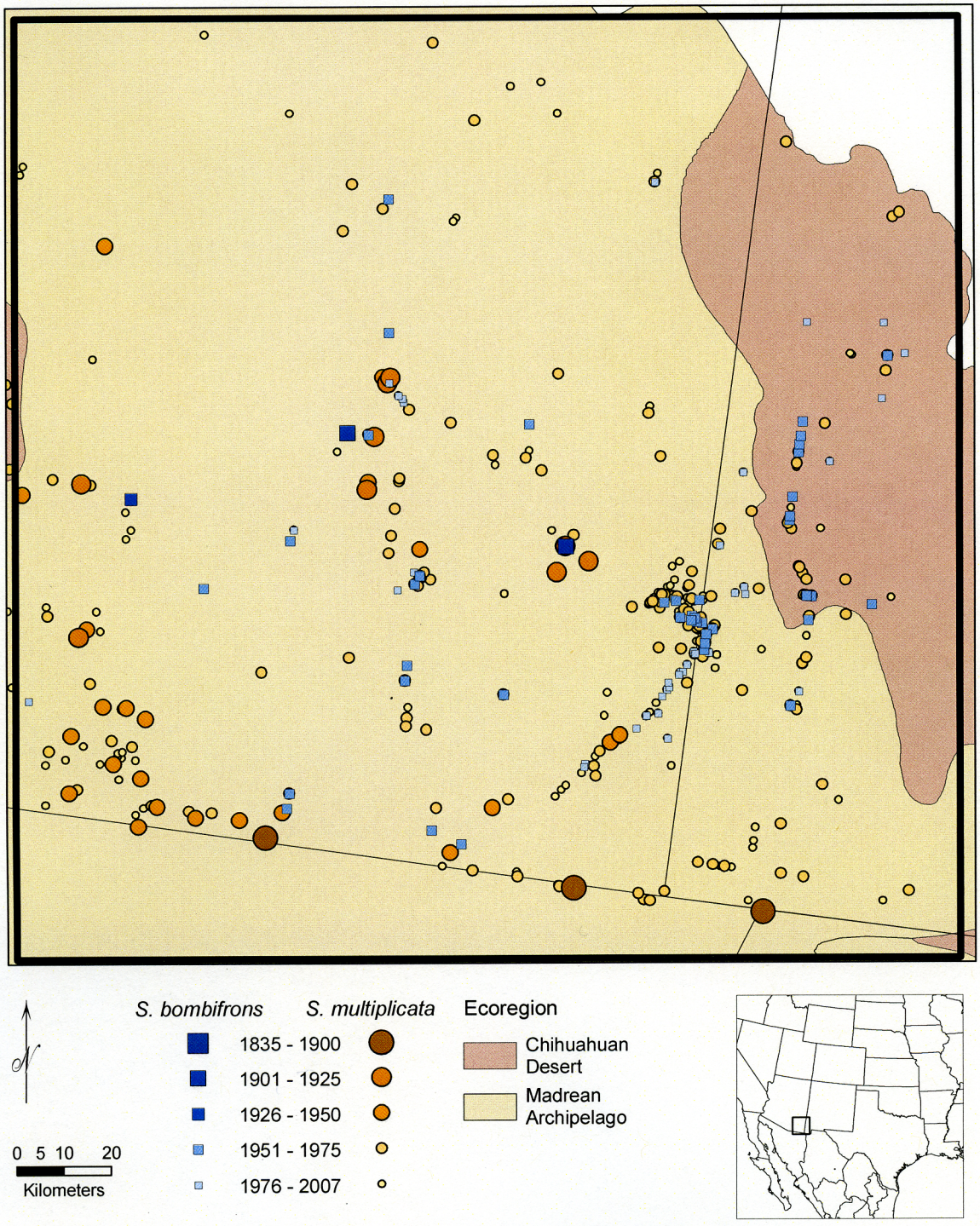

Fig. 3. Zoomed in map of San Simon region. The specific area is shown on the insert map.

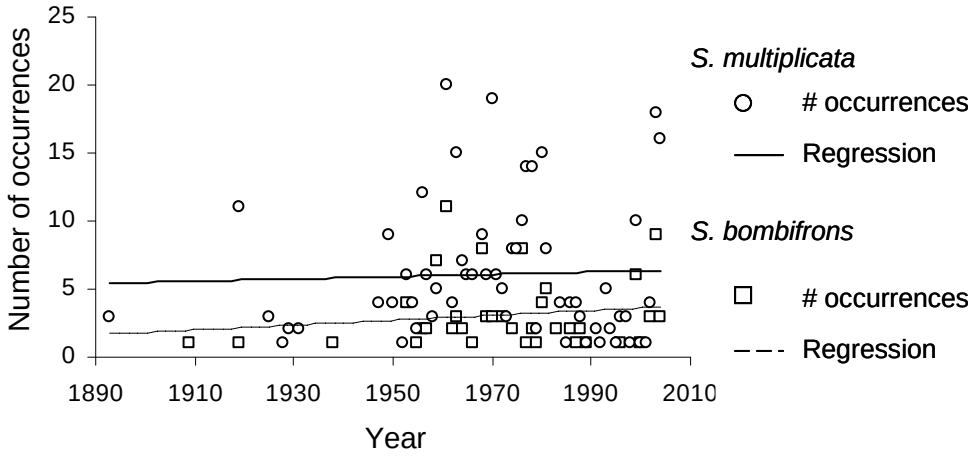

Figure 4. The number of unique collection sites for both *S. bombifrons* and *S. multiplicata* over time within the San Simon population.

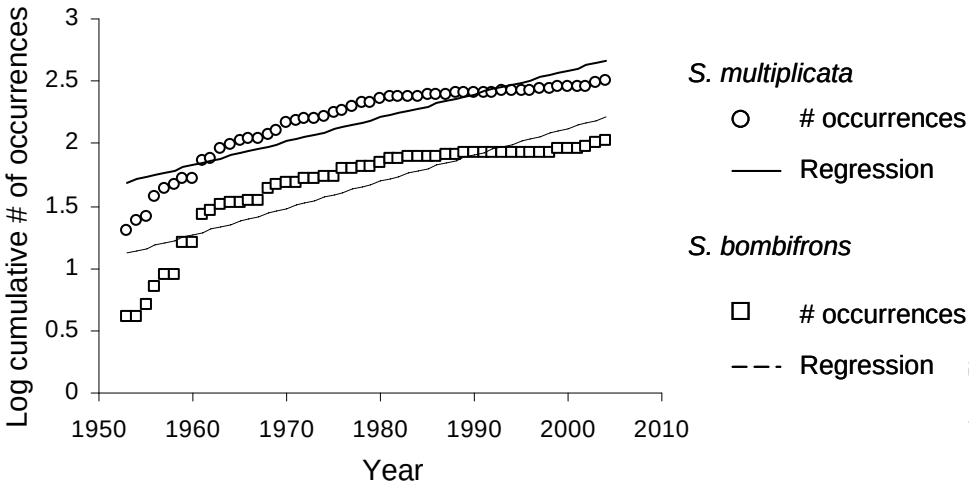

Figure 5. The cumulative log transformed (log10) number of unique collection sites for both *S. bombifrons* and *S. multiplicata* over time within the San Simon population.

CHAPTER V

WHERE THE TWAIN SHALL MEET: DEVELOPING MODELS FOR UNDERSTANDING PATTERNS OF SPECIES CO-OCCURRENCE

Abstract - As ranges are increasingly changing due to deliberate and accidental introductions and global climate change, understanding how both abiotic and biotic factors influence range evolution is becoming increasingly important. Teasing apart the relative contribution of the many different forces that shape ranges is, however, complex. Here, I explore range dynamics of two species of spadefoot toads, *Spea multiplicata* and *S. bombifrons*, which co-occur and potentially hybridize in the southwestern United States. Specifically, I use ecological niche modeling to determine the predicted range of each species based on abiotic factors, and I then identify regions where these two species might co-occur. In doing so, I provide a null model against which the relative contribution of biotic factors to distributions can be tested. I find that the predicted area of potential co-occurrence is smaller than that indicated by current range maps, but larger than predictions based on known patterns of competitive exclusions from a small subset of the region. Finally, I use the results of field surveys to compare actual to predicted distributions in part of the range. I find several pure species sites in areas of predicted co-occurrence, suggesting biotic factors are limiting species distributions. Gaining a better understanding of how different forces shape range dynamics has important implications for targeting field studies, understanding the underlying forces behind species interactions, and for making predictions about how ranges will shift in the future.

INTRODUCTION

Factors determining a species' range are complex, and include both abiotic factors, such as temperature, precipitation, and physical barriers to dispersal, and biotic factors, including availability of food resources, competition, predation, and parasitism (Gaston 2003 and references therein). Understanding how these factors interact to determine the actual range of a species has important implications for understanding range evolution. At the same time, ranges are not static, but rather shift in space over time due to changes in both the abiotic and biotic environment (Gaston 2003). Consequently, as ranges change, novel species interactions can occur (e.g. Elton 1958), introducing new biotic factors that will then continue to shape distributions.

Abiotic factors play an important role in determining ranges. At the most basic level, factors such as temperature and precipitation can set the physical limits to where a species can live. Climate in particular has long been recognized as an important determinant in range limits (e.g. Merriam 1894; Gaston 2003). Recently, shifts in temperature and precipitation due to global climate change have been linked with distributional changes along latitudinal (Parmesan & Yohe 2003) and altitudinal (Lenoir et al. 2008) gradients, providing examples of how important these abiotic factors are at setting range limits.

Abiotic factors are, however, far from the only things that influence range dynamics. Indeed, species interactions can also play a role in determining the distribution and abundance across the range (Darwin 1859; Griggs 1914). The availability of food resources and the presence of predators, competitors, or parasites may determine whether or not a species is present within a habitat that would otherwise be suitable based only on

abiotic conditions (Gaston 2003 and references therein). Competition for resources in particular has been particularly well studied as a force that may limit a species distribution (Hardin 1960; Connell 1961; Davis et al. 1998).

Despite a long tradition of work on species range dynamics, much remains to be learned about the interaction of abiotic and biotic forces in determining both range boundaries and habitat usage within the range. A complicating factor is the potential scale dependence of range dynamics. For example, in Argentine ants, precipitation does not explain species occurrence at a landscape scale, yet soil moisture is very important in explaining species occurrence at a community scale (Menke 2007). The same issue of scale is also relevant when considering species interactions. In *Ulex spp*., Bullock et al. (2000) found that the appearance of co-occurrence between two species disappeared at smaller spatial scales, presumably due to competition for resources.

Determining the relative contribution of biotic and abiotic forces in shaping species distributions at multiple spatial scales is therefore critically important in understanding range dynamics. In particular, determining the factors underlying species co-occurrence can inform studies of both the ecological and evolutionary consequences that result when two closely related species are found in the same habitat. For example, a fundamental principle in ecology posits that two species can not indefinitely occupy the same niche (Gause 1934; Hardin 1960). Thus, when species that are ecologically similar come into contact, selection will act to reduce niche overlap over ecological and, potentially, evolutionary time resulting in either competitive exclusion (Gause 1934; Hardin 1960; Connell 1961) or ecological character displacement (Brown and Wilson 1956; Slatkin 1980). Because both abiotic and biotic factors are important in setting range

limits, both should determine the relative extent to which similar species may co-occur at different spatial scales.

Here, I use two species of spadefoot toads, *Spea multiplicata* and *S. bombifrons*, to test hypotheses about species distributions at multiple spatial scales. As these species have a large potential region of co-occurrence and show interesting patterns in distribution (e.g. Pfennig et al. 2006) and hybridization (Simovich 1985; Pfennig 2007) at a fine spatial scale within one part of their range, this group is an ideal system for examining how fine-scale patterns may translate across the entire range of both species. Specifically, I use ecological niche modeling to predict where each species should occur, and thus, where co-occurrence and potentially hybridization may occur. My general goal is to develop a predictive model of distribution for both species using only abiotic variables. In doing so, I can address important questions about the determinants of range dynamics set up a null model against which predictions about the relative contributions of abiotic and biotic factors to the distribution of a species can be tested.

My specific goals are threefold. First, I aim to determine whether species co-occurrence is predicted to be continuous or patchy throughout the region where both species are found. Based on field work in one subset of the area of range overlap, actual co-occurrence is quite patchy (Pfennig et al. 2006). It is, however, unknown whether this pattern holds throughout the range. Second, I tested whether abiotic factors that were most predictive in the model were similar or different for both species. As these species are closely related, it could be expected that similar abiotic variables are important in predicting occurrences. This pattern would suggest the fundamental niche of both species has been conserved (e.g. Peterson et al. 1999). Alternatively, even closely related species

can show differences in habitat usage (e.g Losos et al. 2003; see Wiens and Graham 2005 for a review of niche conservatism), so that different abiotic factors predict the occurrence of each species. Finally, I used survey results to test whether ecological niche model accurately predicts the distribution of both species.

I tested each of my specific goals using ecological niche modeling both at the level of the entire species distribution and focusing specifically on the area where both species potentially co-occur. These models provide both a guide for directing future field work and a null model against which hypotheses about contribution of biotic factors to the range can be tested.

MATERIALS AND METHODS

Study System

Two species of spadefoot toads, *Spea multiplicata* and *S. bombifrons*, co-occur in much of the southwestern United States. Both species spend most of the year underground, and emerge to breed in ephemeral ponds that form after summer monsoons (Bragg 1965). Because of their reliance on temporary ponds as breeding sites, the ranges of both species should be highly reliant on abiotic environmental conditions that affect pond duration such as temperature and rainfall.

Within the San Simon valley in southeastern Arizona, these species show patterns of either co-occurrence or habitat segregation along an altitudinal gradient (Simovitch 1985; Pfennig et al. 2006). In low elevation playas, only *S. bombifrons* is present. At mid-elevations, both species co-occur. At higher elevation (above 1350 m), only *S. multiplicata* is present (Pfennig et al. 2006). This pattern is likely driven by the

distribution of food resources for tadpoles in the area (Pfennig et al. 2006). When they occur together, *S. bombifrons* tadpoles outcompete *S. multiplicata* tadpoles for one food resource (shrimp), while *S. multiplicata* outcompetes *S. bombifrons* for a second food resource (detritus) (Pfennig and Murphy 2000). When only one food resource is abundant, only the species capable of specializing on that resource is found, whereas when both food resources are abundant, both species are also usually present (Pfennig et al. 2006). Thus, species co-occur in habitats with multiple food resources available (Pfennig et al. 2006) owing to ecological character displacement, but competitive exclusion appears to occur in single resource habitats.

In addition to ecological character displacement, *S. multiplicata* and *S. bombifrons* also show evidence of reproductive character displacement. Although these species are the most divergent within the genus (García-París et al. 2003), hybridization does occur in natural breeding aggregations where these two species co-occur (Simovich 1985; Pfennig and Simovich 2002). Within the San Simon valley, both species show a strong signature of reinforcement; sympatric populations have diverged in female preferences compared to allopatric populations (Pfennig 2000; Pfennig 2007), and hybridization frequency has decreased over a 27 year period of time (Pfennig 2003). Both ecological and reproductive character displacement have thus resulted in interesting patterns of co-occurrence within the San Simon valley.

Although these two species potentially co-occur over a fairly large proportion of their range, little is known about either ecological or reproductive character displacement across most of the area outside of the San Simon region. If food resources are patchily distributed across the range, it could be that competitive exclusion is common throughout

the range. Alternatively, if food resources are distributed more continuously, co-occurrence could be more common in some areas of sympatry than the pattern seen in San Simon.

Patterns in hybridization may also differ throughout the range. In this system, hybrid fitness is likely to be at least partially environmentally dependent (Pfennig 2007). *S. bombifrons* females gain increased development time for their offspring by hybridizing with *S. multiplicata* (Pfennig and Simovich 2002): as such, hybridization may be adaptive for *S. bombifrons* in highly ephemeral ponds (Pfennig 2007). However, hybridization carries some costs, as hybrid offspring have reduced fecundity compared to pure species (Simovich et al. 1991). Therefore, the relative costs and benefits of hybridization should be variable throughout the area of contact between these two species if pond duration is also variable.

In areas of range overlap, we may thus expect to see biotic factors such as ecological and reproductive character displacement resulting in highly variable patterns of exclusion or co-occurrence depending on characteristics of the specific microhabitat.

Niche Modeling

My goals in modeling were to map the predicted range of both species based on abiotic factors. Specifically, I aimed to: 1) determine the predicted spatial distribution and the important abiotic variables contributing to that model across the entire range, 2) use the results of my large scale spatial model to identify areas of likely co-occurrence at a smaller spatial scale, and 3) compare the predicted range using abiotic variables with the known distribution of these species within one well studied subsection of the range. This

later goal allowed us to evaluate the possible role of *biotic* factors (such as competition) in determining local patterns of co-occurrence.

First, I independently determined the predicted range for each species. In doing so, I can both define the spatial extent of the predicted range and evaluate the relative contribution of each abiotic factor included in the model to the model outcome. Second, I looked at the predicted area of co-occurrence that came out of the first model, but at a finer scale. This allows us a more detailed look at where species should be present and at the specific abiotic factors important in predicting co-occurrence. Finally, I compared the distribution of known ponds where either one or both species breed within the San Simon valley to the model predictions. These ponds were not included in the initial model. In doing so, I was able to test whether the model accurately predicted these locations, or alternatively, whether there were differences between the actual and the predicted distribution that could have resulted from biotic interactions.

To determine the potential range of both *Spea multiplicata* and *S. bombifrons*, I first collected locality records from 38 museums across the country. In total, I received 14,695 records for both species. After removing duplicate records, those with missing, incomplete, or inconsistent locality information or year of collection, 1,915 *S. bombifrons* and 2,084
S. multiplicata records remained. Each record was then georeferenced, and I determined the relative accuracy of each locality based on the precision of the description of the collection location.

To determine the predicted distribution for each species, I used the niche modeling program MaxEnt (ver. 3.0.6, Phillips et al. 2006). MaxEnt was chosen over

other modeling algorithms as it requires only presence data rather than presence-absence data (Phillips et al. 2006) (a necessity given the nature of museum records), and because it demonstrates robust model performance compared to other modeling algorithms (Elith et al. 2006). For all models constructed, I kept the default setting of 1 for the regularization multiplier and allowed the program to select the feature type for each environmental layer (Phillips et al. 2006). I also removed duplicate records within a cell to minimize biases due to sampling effort.

MaxEnt uses environmental data and species occurrence records to build a predictive model of species distributions (Phillips et al. 2006). For environmental data, I used altitude and 19 standard bioclimatic variables from Worldclim (www.worldclim.org ver. 1.4; Hijmans et al. 2005; Table 1) at a resolution of 5 km^2 or 1 km^2 depending on the specific model being constructed. Although altitude is often strongly correlated with other bioclimatic variables, I included it in the model as both *Spea spp*. have documented distributions along an altitudinal gradient in the San Simon valley of Arizona (Simovich 1985; Pfennig et al. 2006). The geographic extent of my study area included most of North America to ensure that I captured the range edges for both species. For species occurrence data, I used museum specimens that were accurate in their locality to within a resolution that corresponded with that of the environmental data used, and included only those specimens that had been collected between 1950 – 2000 to correspond with the specific years the primary climate data used to generate the WorldClim environmental layers were collected (Hijmans et al. 2005). The specific details of each model are given below.

Large scale range model

To look at the predicted distribution across the entire range, I independently constructed a model for each species. For environmental data, I used the 20 WorldClim layers mentioned above at a resolution of 5 km^2. After filtering the specimen locality data to include only points accurate to within at least 5 km, and removing duplicate records in MaxEnt, 680 localities for *S. bombifrons* and 541 localities for *S. multiplicata* remained and were used in the model.

In the full model, all localities were used to train the model for each species. Qualitatively, points were fairly equally distributed for both species (Fig 1). As I also removed duplicate records within a cell, biases due to areas that have been disproportionally under- or over-sampled should be minimized. To test the model performance, I re-ran the model for each species 10 times, randomly withholding 75% of the points as test points in each run.

In all models, the predicted range is shown as a gradient, where 0 represents habitat where a species presence is least likely and 1 represents habitat where species presence is most likely. To determine the potential areas of co-occurrence, I projected the resulting full model for both species (where I used all species locality data to train the model) in ArcGIS 9.3. For each species, I then transformed the predicted distribution from a continuous gradient to a binomial distribution where each species is either predicted to be present or absent. To do so, I used a presence-absence threshold set by the model, where the threshold was set at the point where the predicted distribution encompasses 90% of the training points. Areas where both species were predicted to be present were then considered potential areas of co-occurrence.

Fine scale model of predicted co-occurrence

To specifically look at this area of potential co-occurrence in more detail, I created a more fine scale model focusing only on the region encompassing areas of predicted co-occurrence given by the model above. Here, I used the same environmental layers as in the large scale model, but at a resolution of 1 km^2. For species data, I used a subset of the localities used above, including only those locations that both occurred within this region and that were accurate to within at least 1 km. In these models, 250 localities for *S. bombifrons* and 290 localities for *S. multiplicata* were used (Fig. 2).

As above, the full model was generated using every point as training data, and the full model was tested by re-running the model 10 times, withholding a random selection of 75% of records as test points in each run. I again used the model dependent threshold that encompassed 90% of the test points to set the binomial predication for where each species was predicted to be either present or absent. I then mapped the predicted area of co-occurrence by overlaying the areas where both species were predicted to be present.

Case Study: One test of model performance

To test how the model predictions compared to the actual distribution of these species, I used tadpoles collected from 43 ponds throughout and around the San Simon Valley between 1999 and 2004. Tadpoles were genotyped and ponds were then classified as being pure species (either *S. multiplicata* or *S. bombifrons*) or mixed species (containing tadpoles from both species) (see Pfennig and Murphy 2000; Pfennig 2003; Pfennig and Murphy 2003; Rice and Pfennig, in review). I then mapped these pure and

mixed species ponds against the 1km binomial presence/absence model explained above. Comparing whether these ponds fall within predicted areas both tests model performance and provides information about whether biotic factors may extend or limit the actual distribution relative to the predicted distribution. Note that these ponds were not used in constructing the niche model, to avoid a lack of independence between model and test points.

RESULTS

For each model, I evaluated both the spatial distribution of the predicted range, and the abiotic factors that contributed to the model. Specific results of each model are outlined below.

Large scale range model

Interesting patterns in distribution emerged from these models. For the complete model looking at predicted habitat across the range, I found that areas predicted to have a high probability of species occurrence include much of the central United States for *S. bombifrons*, with the southern edge of the most likely range occurring along the southern edge of Arizona and New Mexico. The model also identified a southern Texas population that is isolated from the rest of the range by an area of low habitat suitability (Fig 1a). Areas predicted as highly suitable for *S. multiplicata* occurred through most of the southwestern US and through the central region of Mexico (Fig 1b).

After converting the continuous prediction to a binomial model of predicted presence vs. absence using the threshold given by the model for each species, I found that

overlaying the areas of predicted presence for each species shows a large region where both species are predicted to co-occur (Fig. 3a). Looking at the western edge of the predicted region of co-occurrence shows strong patchiness in where both species are expected. In other regions, however, such as northern Texas and parts of northern Arizona, predicted areas of co-occurrence are far more continuous (Fig 3b).

When considering which environmental factors were most important in model performance, I found that the top predictive variables differed for each species. I a priori decided to consider factors contributing at least 5% to be important in the model outcome. For *S. bombifrons*, seven variables met this 5% threshold: 1) mean temperature of the wettest quarter, 2) maximum temperature of the warmest month, 3) temperature annual range, 4) precipitation of the coldest quarter, 5) mean diurnal range in temperature, 6) minimum temperature of the coldest month, and 7) annual mean temperature. Combined, these seven variables accounted for 89.2% of the predictive value of the model (Table 2). For *S. multiplicata*, five variables contributed at least 5% to the model: 1) mean diurnal range in temperature, 2) isothermality, 3) mean temperature of the wettest quarter, 4) altitude, and 5) mean temperature of the driest quarter. Together, these five variables contributed 86.9% to the model outcome (Table 2).

Fine scale model of predicted co-occurrence

Focusing exclusively on the region where both species were predicted to co-occur by the model above at a 1 km resolution (Fig 2) shows the area in the best predicted class is substantially less than that predicted under the 5km model. In looking at the presence/absence model showing the specific areas where co-occurrence is most likely, I

again see the western edge is patchy, with a more continuous distribution of predicted co-occurrence in northern Texas and eastern New Mexico (Fig 4). As models using more fine-scale grain size tend to perform better than coarser resolution data (Guisan et al. 2007), the areas highlighted in this model should be the most likely regions for finding these species.

As here I am looking only at regions where both species could potentially co-occur, rather than across the range as above, I expect the abiotic factors important in predicting the range of each species in this model should be those that are most useful in predicting actual co-occurrence. For *S. bombifrons*, the top 6 variables each contributed at least 5% to the model: 1) precipitation of driest quarter 2) mean temperature of the coldest quarter, 3) temperature annual range 4) isothermality 5) altitude, and 6) precipitation of the driest month. Together, these results contributed 81.3% of the model performance (Table 3). For *S. multiplicata*: 1) altitude, 2) temperature annual range, 3) temperature seasonality, 4) precipitation of the driest month, 5) annual mean temperature, 6) isothermality, 7) precipitation of the coldest quarter, 8) minimum temperature of the coldest month, and 9) precipitation of wettest month each contributed at least 5% to the model, and together account for 89.2% of the model performance (Table 3).

When comparing the abiotic factors that contributed to both the large and small scale models, I see several differences as I expected. At the fine scale, I am considering a much smaller area, that is, just the region of predicted co-occurrence, than the large scale model that was projected over the entire range of each species. Therefore, the large scale model identifies variables that are important in predicting the entire range, while the finer

scale model should identify factors that are specifically important in this subset of the range.

For both large and fine scale models, model performance was robust across the multiple test runs even with the relatively high percentage of points used to test the model (75%) vs. those used in model training (25%). Maps produced were qualitatively consistent, and the top predictive values were very similar in each iteration of the model for both the large scale models across the range and the smaller scale models within the region of co-occurrence. As the results for each model are so consistent between test runs, the maps produced should provide a robust measure of potential species distributions based on the environmental layers that went in to the model. Furthermore, these consistent results strongly suggest that the model outcomes were not unduly being biased by the specific species occurrence records that went in to each model.

Case Study: One test of model performance

In total, I included 43 ponds, of which one was pure *S. bombifrons*, 28 were pure *S. multpilicata,* and 14 were mixed ponds with both species present. Looking at the map of ponds by altitude shows that *S. bombifrons,* from both pure and mixed species ponds, is present only below 1370 meters, with 14 of 15 ponds occurring below 1350 m as expected based on previous surveys (Simovich 1985; Pfennig et al. 2006) (Fig 5a). *S. multiplicata* were found across a much wider altitudinal range, with the highest pond occurring at 1600 m, and several ponds occurring above 1400 m (Fig 5a). Looking specifically at an area surrounding the mixed species ponds, we can more clearly see pure *S. multiplicata* ponds at higher elevations than mixed species ponds (Fig 5b).

When I compare the presence/absence model of *S. bombifrons* to the distribution of ponds, I find that all ponds with *S. bombifrons* (both pure species and mixed species ponds) were found in areas predicted as good *S. bombifrons* habitat (Fig. 6a). Looking at the presence/absence model for *S. multiplicata* shows that all *S. multiplicata* ponds also are found within areas predicted to have that species (Fig. 6b). Interestingly, looking at areas where both species are predicted to occur shows that all mixed species ponds fell in this region (Fig. 7a). At the same time, however, several pure species ponds were also found in areas of predicted co-occurrence. Specifically looking at the region surrounding the area of mixed species ponds shows 12 pure *S. multiplicata* were found in areas predicted to have both species (Fig 7b). Of these ponds, all came within at least 12 km of a mixed species ponds, and some pure and mixed species ponds were separated by a distance of only 2km.

DISCUSSION

Understanding the complex forces underlying range dynamics is an important step in studying not only range evolution, but also the evolutionary consequences of species interactions. Determining the relative contributions of biotic and abiotic forces to range dynamics provides a better understanding of species distributions and also yields a foundation for predicting how ranges will change in the future.

Both abiotic and biotic factors contribute to range dynamics (Gatson 2003; Menke et al. 2007). The combination of every biotic and abiotic factor important to a species results in the final distribution of the species, and shapes how the range will shift in space over time. When the distribution of one species shifts in such a way that it begins to

overlap with an ecologically similar species, this can result in new biotic interactions that in turn can continue to influence each species new distribution. For example, when two species utilize the same resources, either competitive exclusion (Gause 1934; Hardin 1960; Connell 1961) or ecological character displacement (Brown & Wilson 1956; Slatkin 1980) can occur. Competitive exclusion and ecological character displacement each result in different spatial distributions. Competitive exclusion often leads to spatial segregation of the habitat, such that the two species are never actually found in the same habitat (e.g. Connell 1961; MacArthur 1958). Alternatively, ecological character displacement often results in both species occurring in the same habitat, but utilizing different resources within that habitat (e.g. Pfennig and Murphy 2000; Schluter and McPhail 1992).

As with competitive exclusion, sexual exclusion, the displacement of one species due to reproductive interference, can lead to spatial segregation of the habitat (Chunco Chapter 3; Hochkirch et al. 2007; see also Gröning and Hochkirch 2008 and references therein). Alternatively, reproductive character displacement can result in species co-occurrence within a habitat (Howard 1993; Coyne and Orr 2004). To complicate matters, hybridization may not operate in the same way everywhere two populations come together. For example, if hybrid fitness is environmentally dependent, the outcome of hybridization may vary throughout a region depending on the fitness of hybrid offspring (Arnold 1997; Pfennig 2007). Therefore, studies across the entire area of secondary contact are vitally important.

Here, I used spadefoot toads a case study for examining patters of species distributions. Spadefoots are an ideal system for studying distributions at multiple scales.

As amphibians that rely on ephemeral pools to breed (Bragg 1965), their distribution is controlled, at least in part, by temperature and precipitation. At the same time, strong evidence suggests that competition has resulted in competitive exclusion and character displacement (Pfennig et al. 2006), as well as reinforcement (Pfennig 2003), in one region where the two species are both found. However, little is known about the distribution of these species across most of their range.

I began by constructing predictive maps of the entire range and within just the area of predicted co-occurrence for both *S. multiplicata* and *S. bombifrons*. Looking at the predicted distribution and determining areas where both species are most likely to occur provides target areas for future field studies. As both species occur over fairly large ranges, and because they are only active for a few weeks a year (Bragg 1965), targeting areas where each species is most likely to be found can be immensely useful for increasing the probability of finding toads during field surveys.

Additionally, these maps can provide useful information for testing specific ecological and evolutionary hypotheses. For example, species interactions may be differ depending on the relative abundance of interacting species (e.g. Peterson et al. 2005). Also, species interactions will differ depending on the length of time they have been in contact (e.g. Borge et al. 2005). In identifying the relative suitability of the habitat around and in areas where co-occurrence is most likely, I can make rough predictions about the relative abundance of each species. Here, *S. bombifrons* should be more common than *S. multiplicata* at the northern edge of the area of co-occurrence, while the reverse is likely to be true at the southern edge. Comparing populations from the edges of the region of co-occurrence and from the core areas can provide important information on the true

distributional patters of these species. More interestingly, these populations can then be used to test the degree to which each species in each population shows signs of character displacement and reinforcement, providing better information on how ecology contributes to these processes, and potentially suggesting differences in how long each of these populations have been in secondary contact with the other species.

When considering the abiotic factors that contribute to each model across the entire range, there are interesting similarities and differences between both species. Unsurprisingly, mean temperature of the wettest quarter, the only time of the year when these species are active, was important in the model for both species. The mean diurnal range in temperature was also important for both species. While these were the only two factors that were important in both models at this scale, it is important to note that nearly all factors in both models involved some aspect of temperature. Therefore, temperature appears to be more important for predicting both species' distributions than precipitation, even though the specific components of temperature that were important in the models differed between these species.

When considering abiotic variables contributing to the 1km model within the predicted region of co-occurrence, I see far more similarity between the two species than in the entire range model above. This is expected, as the area being evaluated was substantially smaller, and both species were predicted to occur (to a greater or lesser extent) throughout the area, so the environmental gradients in abiotic variables were shared by both species. Here, I also see precipitation becomes important in predicting species occurrence, indicating that this variable might be more important in predicting co-occurrence than in predicting the total range for these species.

Looking at where co-occurrence is predicted in the range model shows strong patchiness at the western edges of this region (Fig 3), and a far more continuous distribution in the east. Interestingly, the area around San Simon, where co-occurrence is known to be patchy, does indeed show patchiness in predicted co-occurrence. This area corresponds with the western and southern most edge of the range for *S. bombifrons.* As such, we should expect that *S. bombifrons* is rarer and potentially more patchily distributed than *S. multiplicata*, and a study of habitat occupancy of both species supports this pattern (Chunco Chapter 4). Therefore, this patchy distribution of co-occurrence could simply reflect the patchy distribution of *S. bombifrons* in this region. The eastern edge of the predicted area of co-occurrence is far more continuous, even though this area represents the northern and eastern edge of the range for *S. multiplicata*. This may suggest that the distribution of *S. multiplicata* is more continuous at this range edge than *S. bombifrons* is at the western range edge. This difference leads to interesting questions about what is determining co-occurrence between these species throughout the habitat. Further research on the distribution of food resources, the strength of competition between these species, and the length of co-occurrence throughout this region are clearly needed to fully understand the range dynamics in this region.

Looking at the known species occurrences mapped over predictions of the model, I find that the 1km model does accurately predict both pure and mixed species ponds (Fig 6). At the same time, I find several pure *S. multiplicata* ponds that occur within an area predicted to have both species present, and some of these pure species ponds are found within only 2 km of mixed species ponds (Fig 7). Therefore, *S. bombifrons* is present in the region, but is absent from several, potentially good breeding sites. Numerous reasons

could explain why a species is missing from a habitat that seems suitable, including physical barriers to dispersal, microclimatic differences at a scale too small to be detected by the model, or biotic factors including the presence or absence of food resources, predators, or competitors. As within this area there are no obvious physical barriers to dispersal, and the physical conditions around these pond are similar, (pers. obs.), biotic forces are likely the driving force for this pattern. As competition for food resources is know to affect local distributions, my results correspond with the findings that competitive exclusion is driving this pattern (Pfennig et al. 2006).

By building robust models of the distribution of each species based on abiotic environmental variables, I have established a null model against which the relative contribution of biotic variables can now be tested. Surveying populations within and outside the area of predicted co-occurrence can reveal how important biotic variable may be in driving distributions of these species. For example, both species are predicted to occur continuously over a large portion of the eastern region of predicted co-occurrence. If targeted field surveys reveal that true distributions are more patchily distributed in this area, competitive exclusion may play a key role in determining habitat occupancy in this area. Alternatively, if populations do routinely co-occur, testing for evidence of ecological and reproductive character displacement can provide insights into why co-occurrence is more common in this region than in San Simon.

Here, I used two common species that has been well studied in one region of their ranges to determine how small scale species distributions may scale up across their entire distributions. This work provides a foundation for future field studies and experiments that can disentangle the influence of abiotic and biotic factors at shaping range dynamics.

ACKNOWLEDGEMENTS

I would first like to thank the many museums and curators who were essential to this project. Also, Amanda Henley provided invaluable technical help using ArcGIS, Todd Jobe, Jennifer Costanza, Matt Simon, Anne Trainor, and Ian Breckheimer provided feedback on MaxEnt results, and members of the Pfennig lab including Laura Exline, Elizabeth Wojtowicz, Sarah Seiter, and Sumit Dholé provided valuable comments that greatly improved the manuscript. Finally, members of my committee including Maria Servedio, Aaron Moody, Joel Kingsolver, and David Pfennig greatly contributed to the development of this project.

REFERENCES

Arnold, M. L. 1997. Natural hybridization and Evolution. Oxford Univ. Press, Oxford.

Borge, T., K. Lindroos, P. Nádvorník, A.-C. Syvänen, and G.-P. Sætre. 2005. Amount of introgression in flycatcher hybrid zones reflects regional difference in pre and post-zygotinc barriers to gene expression. J. Evol. Biol. 18, 1416-1424.

Bragg, A. N. 1965. Gnomes of the night: the spadefoot toads. University of Pennsylvania Press, Philadelphia, Pennsylvania, USA.

Brown, W. L. and E. O. Wilson. 1956. Character displacement. Systematic Zoology 5, 49-64.

Bullock, J. M., R. J. Edwards, P. D. Carey, R. J. Rose. 2000. Geographical separation of two *Ulex* species at three spatial scales: does competition limit species ranges? Ecography 23, 257-271.

Connell, J. H. 1961. The influence on interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42, 710-723.

Coyne, J. A. and H. A. Orr. 2004. Speciation. Sinaure, Sunderland, MA.

Darwin, C. 1859. On the origin of species by means of natural selection. John Murry, London.

Davis, A. J., L. S. Jenkinson, J. H. Lawton, B. Shorrocks, & S. Wood. 1998. Making mistakes when predicting shifts in species range in response to global warming. Nature 391, 783-786.

Elith J. et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 2, 129-151.

Elton, C. S. 1958. *The Ecology of Invasions by Animals and Plants*. University of Chicago Press, Chicago.

García-París, M., D. R. Buchholz, and G. Parra-Olea. 2003. Phylogenetic relationships of Pelobatoidea re-examined using mtDNA. Molecular Phylogenetics and Evolution 28, 12-23.

Gaston, K. J. 2003. *The structure and dynamics of geographic ranges.* Oxford University Press.

Gause, G. F. 1934. *The struggle for existence*. Williams and Wilkins, Baltimore, Maryland, USA.

Gröning, J. and A. Hochkirch. 2008. Reproductive interference between animal species. Quart. Rev. Biol. 83, 257-282.

Griggs, R. F. 1914. Observations on the behavior of some species at the edges of their ranges. Bull. Torrey Bot. Club. 41, 25-49.

Guisan, A., C. H. Graham, J. Elith, F. Huettmann, and the NCEAS Species Distribution Modeling Group. Sensitivity of predicted species distribution models to change in grain size. Diversity Distrib. 13, 332-340.

Hardin, G. 1960. The competitive exclusion principle. Science 131, 1292-1297.

Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. International J. Climatology 25, 1965-1978.

Hochkirch, A., J. Gröning, A. Bücker. 2007. Sympatry with the devil: reproductive interference could hamper species coexistence. J. Anim. Ecol. 76, 633-642.

Howard, D. J. 1993. Reinforcement: origin, dynamics, and fate of an evolutionary hypothesis. Pp. 46-69 in R. G. Harrison, ed. Hybrid zones and the evolutionary process. Oxford Univ. press, New York.

Lenoir, J., J. C. Gégout, P. A. Marquet, P. de Ruffray, H. Brisse. A significant upward shift in plant species optimum elevation during the 20th century. Science 320, 1768-1771.

Losos, J. B., M. Leal, R. E. Glor, K. de Queiroz, P. E. Hertz, L. R. Schettino, A. C. Lara, T. R. Jackman, A. Larson. 2003. Niche lability in the evolution of a Caribbean lizard community. Nature 424, 542-545.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39, 599-619.

Menke, S. B., R. N. Fisher, W. Jetz, and D. A. Holway. 2007. Biotic and abiotic controls of Argentine ant invasion success at local and landscale scales. Ecology 88, 3164-3173.

Merriam, C. H. 1894. Laws of temperature control the geographic distribution of terrestrial animals and plants. National Geographic 6, 229-238.

Parmesan, C. & G. Yohe. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37-42.

Peterson, A. T., J. Soberón, V. Sánchez-Cordero. 1999. Conservatism of ecological niches in evolutionary time. Science 285, 1265-1267.

Peterson, M. A., B. M. Honchak, S. E. Locke, T. E. Beeman, J. Mendoza, J. Green, K. J. Buckingham, M. A. White, K. J. Monsen. 2005. Relative abundance and the species-specific reinforcement of male mating preference in the *Chrysochus* (Coleoptera: Chrysomelidae) hybrid zone. Evolution 59, 2639-2655.

Pfennig, D. W. and P. J. Murphy. 2000. Character displacement in polyphonic tadpoles. Evolution 54, 1738-1749.

—. 2003. A test of alternative hypotheses for character divergence between coexisting species. *Ecology*, 84:1288-1297.

Pfennig, K. S. 2000. Female spadefoot toads compromise on mate quality to ensure conspecific matings. Beh. Ecol. 11, 220-227.

Pfennig, K. S. 2003. A test of alternative hypotheses for the evolution of reproductive isolation between spadefoot toads: support for the reinforcement hypothesis. Evolution 57, 2842-2851.

Pfennig, K. S. 2007. Facultative mate choice drives adaptive hybridization. Science 318, 965-967.

Pfennig, K. S. and M. A. Simovich. 2002. Differential selection to avoid hybridization in two toad species. Evolution 56, 1840-1848.

Pfennig, D. W., A. M. Rice & R. A. Martin. 2006. Ecological opportunity and phenotypic plasticity interact to promote character displacement and species coexistence. Ecology 87, 769-779.

Phillips, S. J., R. P. Anderson, R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecol. Modelling 190, 231-259.

Schluter, D. and J. D. McPhail. 1992. Ecological character displacement and speciation in sticklebacks. Am. Nat. 140, 85-108.

Simovich, M. A. 1985. Analysis of a hybrid zone between the spadefoot taods *Scaphiopus multiplicataus* and *Scaphiopus bombifrons*. Ph.D. diss., University of California, Riverside, CA.

Simovich, M. A., C. A. Sassaman, A. Chovnick. 1991. Post-mating selection of hybrid toads (*Scaphiopus multiplicatus* and *Scaphiopus bombifrons*). Proc. San Diego Soc. of Nat. Hist. 1991, 1-6.

Slatkin, M. 1980. Ecological character displacement. Ecology 61, 163-177.

Stebbins, R. C. 2003. A Field Guide to Western Reptiles and Amphibians: Peterson Field Guides. New York, Houghton Mifflin Company.

Wiens, J. J. and C. H. Graham. 2005. Niche conservatism: Integrating evolution, ecology, and conservation biology. Annu. Rev. Ecol. Evol. Syst. 36, 519-539.

Table 1. Variables used in all niche models. Data from WorldClim (http://worldclim.com/). For details, see Hijmas et al. (2005).

Variable	**Calculation for derived variables**
Annual Mean Temperature	
Mean Diurnal Range in Temperature	Mean of Monthly (Maximum Temperature - Minimum Temperature)
Isothermality	Mean Diurnal Range in Temperature/ Temperature Annual Range * 100
Temperature Seasonality	Standard Deviation in Temperature * 100
Maximum Temperature of Warmest Month	
Minimum Temperature of Coldest Month	
Temperature Annual Range	Maximum Temperature of Warmest Month - Minimum Temperature of Coldest Month
Mean Temperature of Wettest Quarter	
Mean Temperature of Driest Quarter	
Mean Temperature of Warmest Quarter	
Mean Temperature of Coldest Quarter	
Annual Precipitation	
Precipitation of Wettest Month	
Precipitation of Driest Month	
Precipitation Seasonality	Coefficient of Variation in Precipitation
Precipitation of Wettest Quarter	
Precipitation of Driest Quarter	
Precipitation of Warmest Quarter	
Precipitation of Coldest Quarter	
Altitude	

Table 2. The relative contribution of abiotic variables contributing at least 5% to the predictive model across the range at a 5km resolution for both *S. bombifrons* and *S. multiplicata*. Factors in common between the species are marked with an *.

S. bombifrons

Variable	**Percent Contribution**
*Mean Temperature of Wettest Quarter	27.2
Maximum Temperature of Warmest Month	19.8
Temperature Annual Range	12.8
Precipitation of Coldest Quarter	9.8
*Mean Diurnal Range in Temperature	8.2
Minimum Temperature of Coldest Month	6.1
Annual Mean Temperature	5.3
Total Contribution to Model:	89.2

S. multiplicata

Variable	**Percent Contribution**
*Mean Diurnal Range in Temperature	36.6
Isothermality	15.6
*Mean Temperature of Wettest Quarter	13.9
Altitude	10.4
Mean Temperature of Driest Quarter	10.4
	86.9
Total Contribution to Model:	86.9

Table 3. The relative contribution of abiotic variables contributing at least 5% to the predictive model within the region of co-occurrence at a 1km resolution for both *S. bombifrons* and *S. multiplicata*. Factors in common between the species are marked with an *.

S. bombifrons

Variable	**Percent Contribution**
Precipitation of Driest Quarter	35.6
Mean Temperature of Coldest Quarter	13.8
*Temperature Annual Range	11.8
*Isothermality	9.1
*Altitude	5.9
*Precipitation of Driest Month	5.1
Total Contribution to Model:	81.3

S. multiplicata

Variable	**Percent Contribution**
*Altitude	17.6
*Temperature Annual Range	15.6
Temperature Seasonality	12.4
*Precipitation of Driest Month	11.6
Annual Mean Temperature	9
*Isothermality	6.6
Precipitation of Coldest Quarter	5.7
Minimum Temperature of Coldest Month	5.5
Precipitation of Wettest Month	5.2
Total Contribution to Model:	89.2

5 Km Resolution Range Model

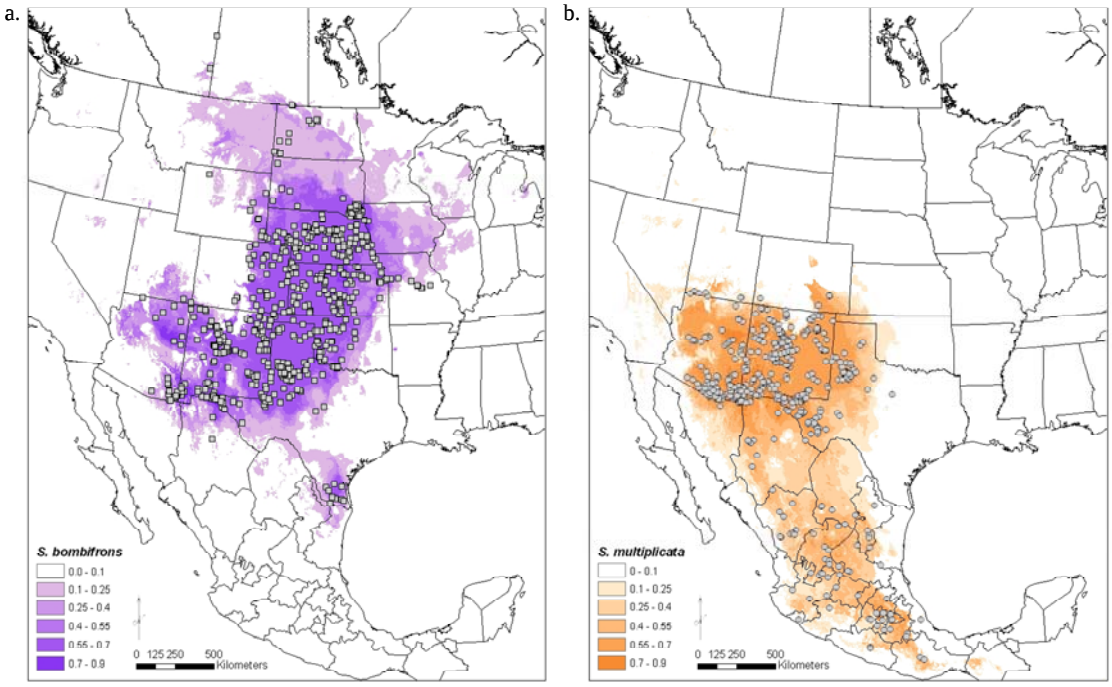

Fig. 1. The predicted distribution *S. bombifrons* (a) and *S. multiplicata* (b) across the range using environmental and point data at a 5 km resolution. Localities used to construct the ecological niche model are shown as gray points for both species.

1 Km Resolution Co-occurrence model

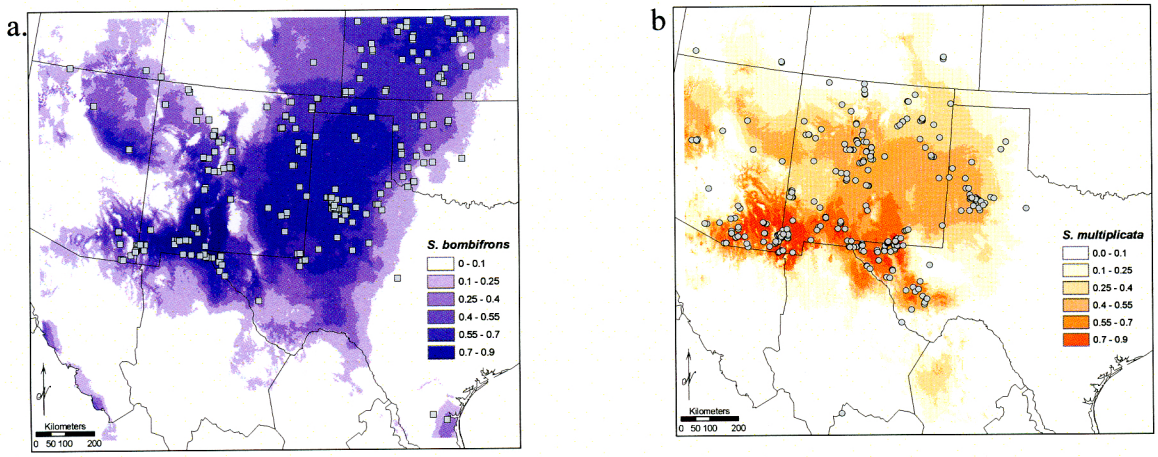

Fig 2. The predicted distribution *S. bombifrons* (a) and *S. multiplicata* (b) within the region of predicted co-occurrence (given by the model of the entire range) using environmental and point data at a 1 km resolution. Localities used to construct the ecological niche model are shown as gray points for both species.

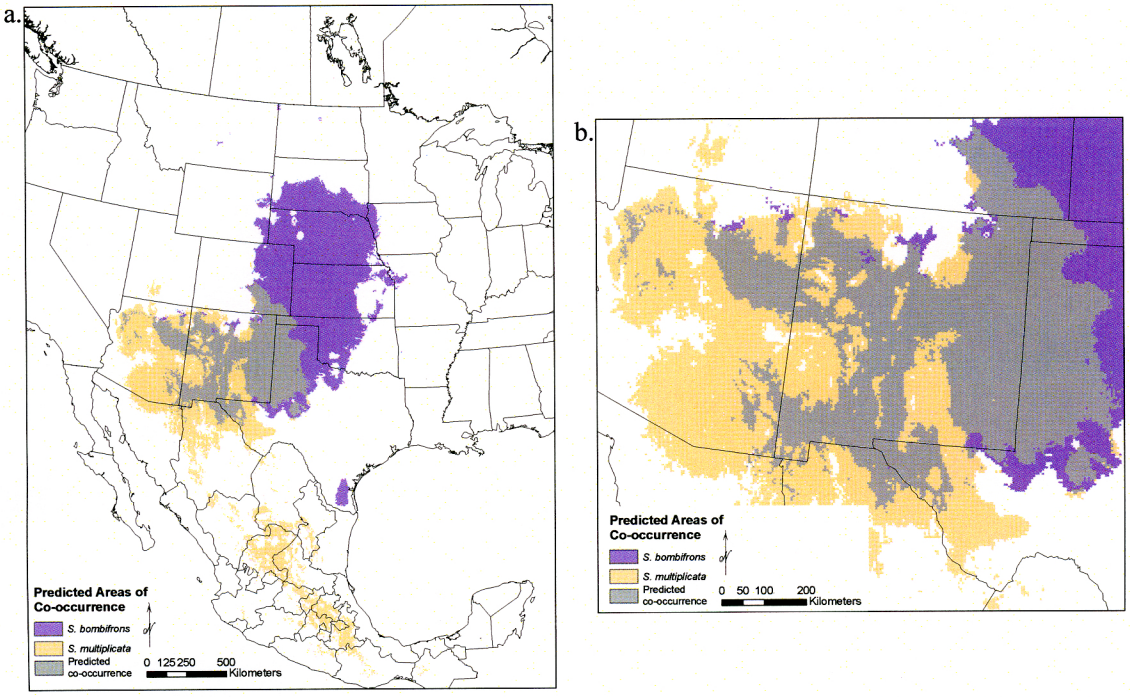

Fig 3. Areas of predicted co-occurrence between *S. multiplicata* and *S. bombifrons* using data at a 5km resolution. Each individual species' best predicted range is shown, and areas where these two ranges overlap are considered likely regions of co-occurrence. Both the total range (a) and a zoomed in map of the area of predicted co-occurrence (b) are shown.

1 Km Resolution Presence/Absence Co-occurrence Model

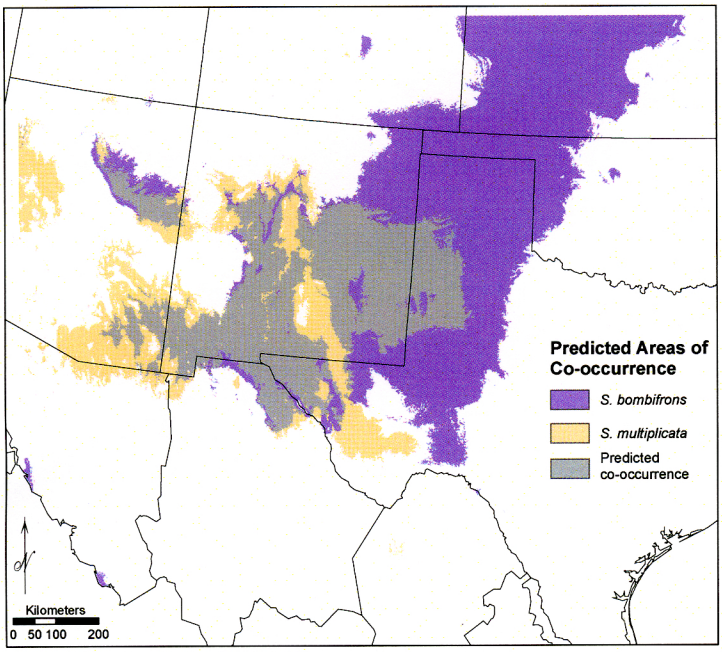

Fig 4. The predicted distribution of *S. bombifrons*, *S. multiplicata*, and both species using a 1km resolution, within the area predicted to have both species as identified in the range model in Fig 3

Test Ponds and Altitude

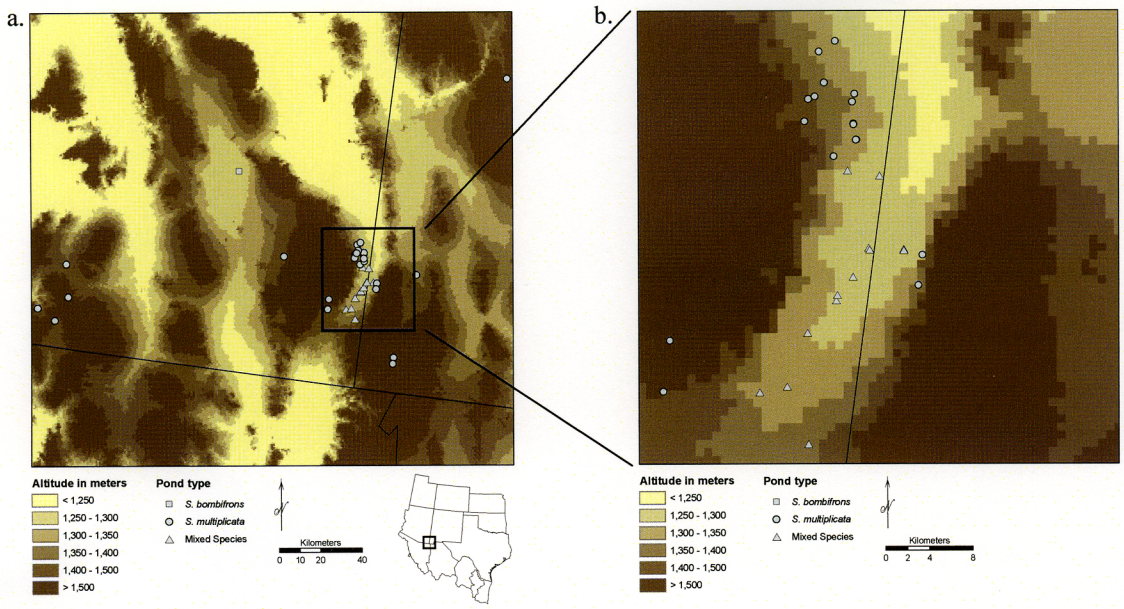

Fig 5. All test ponds mapped by altitude (the specific region is shown as a box on the insert map) (a), and a zoomed in view of the mixed species ponds and surrounding area (b).

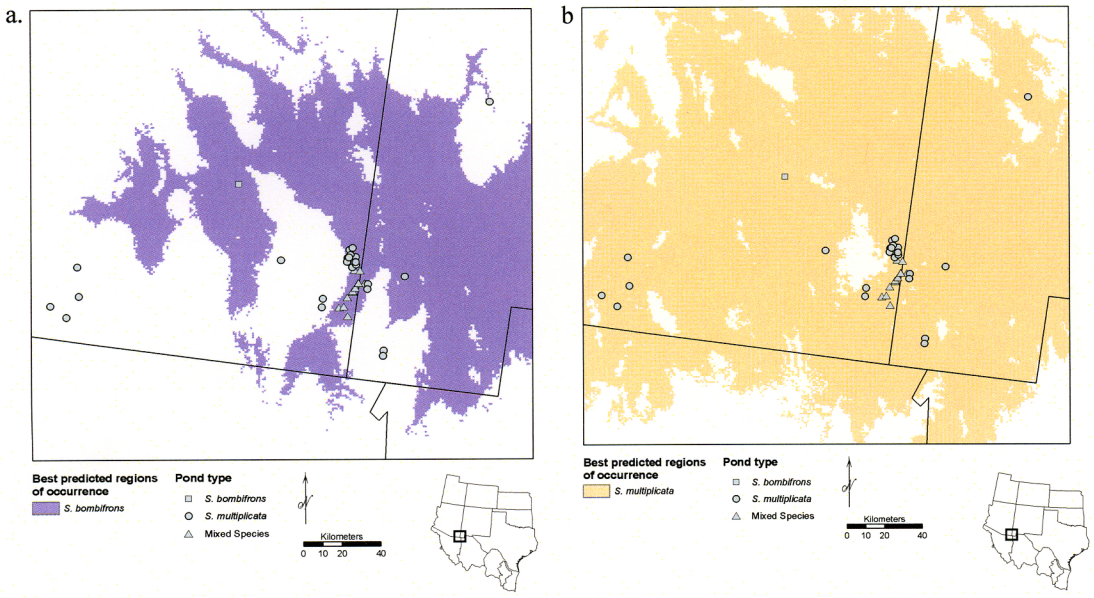

Fig 6. The location of test ponds mapped on the prediction of best habitat for *S. bombifrons* (a) and *S. multiplicata* (b).

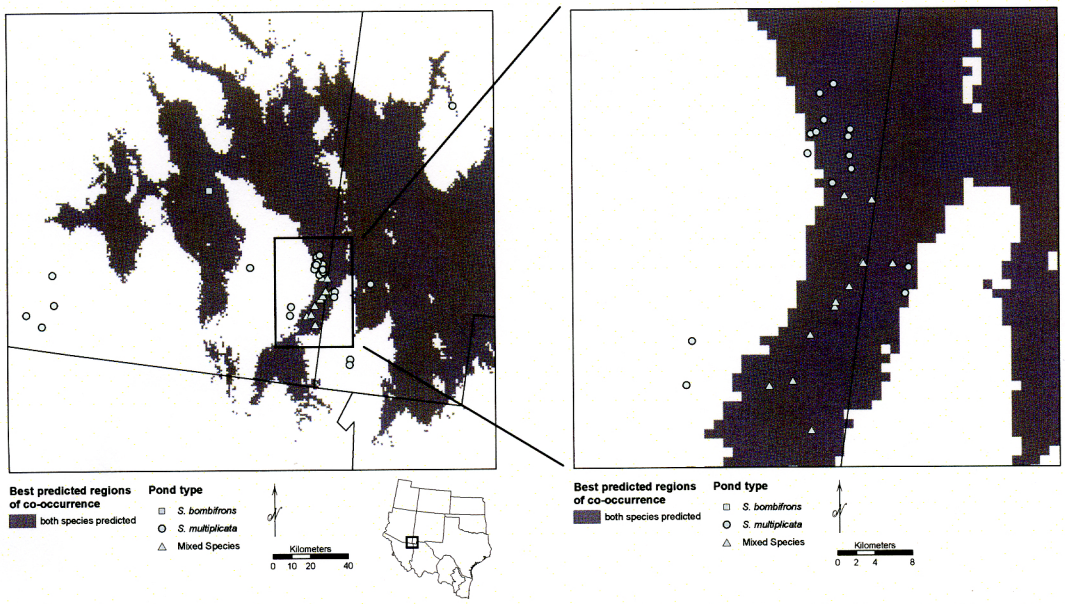

Fig. 7. Test ponds mapped over the predicted areas co-occurrence in southeastern Arizona (a) and specifically around an area where mixed species ponds are common (b).

CHAPTER VI

CONCLUSIONS

In this work, I have evaluated how habitat heterogeneity can contribute to ecological patterns of species distribution and abundance. I have also investigated the role of habitat heterogeneity in the processes of phenotypic evolution and extinction. In doing so, my goal was to demonstrate how habitat variation influences ecological and evolutionary processes at multiple biological and geographic scales.

First, in a single population, it is important to consider how even microhabitat variation, that is, variation at a scale such that a single individual can move between habitats, can have evolutionary consequences. In Chapter 2, I use a biologically plausible model to explore the effects of habitat on male color polymorphisms. When the microhabitat affects sexual and natural selection, this can indeed lead to polymorphism maintenance. As the habitat becomes more homogeneous (that is, as one habitat type predominates), polymorphism is more likely to be lost. While this model lays the groundwork for addressing the role of the microhabitat in maintaining polymorphism, it also raises interesting questions. For example, polymorphisms may often precede sympatric speciation (Gray and McKinnon 2007), but how and when they are likely to do so remains unclear. Determining the conditions under which microhabitat variation contributes to speciation – rather than the persistent maintenance of polymorphisms

within a species – is critical for understanding the conditions under which sympatric speciation occurs.

When multiple populations live in different habitats, these environmental differences can lead not only to evolutionary divergence, but also to ecological differences that place populations at differential risk of extinction. In Chapter 3, I specifically considered how the environment can affect female mate choice and I described some of the consequences those choices can have for population viability. I suggested the effects of female mate choice on population persistence can be important in explaining both ecological patterns of distribution and abundance and evolutionary patterns of diversity. While a few empirical examples of the role of mate choice on population viability are starting to emerge (e.g. Hochkirch et al. 2007), most work in this field remains theoretical. Important work remains to be done to determine the specific conditions that may result in differential extinction risk. For example, studies that measure reproductive rates and population growth that result from given mate choice patterns would go far to elucidating how sexual selection impacts population growth, persistence, and ultimately, extinction risk.

At the scale of the entire range of a species, the environment plays an important role in driving both patterns of distribution and abundance within the range and in setting the boundaries of the range. Currently, anthropogenic change is affecting both of these properties of species distributions (Hsieh et al. 2009). In Chapter 4, I used museum collections to explore past distributions in two species of spadefoot toads. In these species, land-use change was expected to have impacted both the range extent and the distribution of at least one species. Instead, I found no clear signature of shift in range

extent or distribution in either species over the last 100 years. One interpretation of this result is that these species have not been affected by land use in terms of distribution or habitat occupancy. However, drawing conclusions from this work remains challenging because of the difficulty in disentangling the effects of sample effort from true distributional patterns. Rather than suggesting that land-use does not affect these species, I instead suggest that this work reveals a need for more consistent and systematic documentation of species occurrences in general. At the same time, little is known about either dispersal ability or population dynamics in spadefoot toads even though these are common and widely distributed. A better understanding of these processes will be important both in improving knowledge of this system and for using spadefoot toads as a model for understanding how anthropogenic change impacts amphibian communities.

Finally, I also considered species interactions. When ecologically similar species compete for resources, the result is usually either competitive exclusion (Gause 1934; Hardin 1960) or character displacement (Brown and Wilson 1956; Slatkin 1980). To understand these processes, it is essential to first determine how the physical environment contributes to the spatial distribution of the interacting species. In Chapter 5, I used ecological niche modeling to create distribution maps of two species of spadefoot toads based only on abiotic environmental variables. I then tested how well the model predicted known populations. I found that some regions predicted to have both species instead had only one species, potentially indicating the importance of biotic factors in driving distributions. This model provides testable hypotheses about factors underlying species interactions. Field and experimental studies will, however, be essential to fully understand how biotic and abiotic factors contribute to these interactions.

In these last two chapters, species records from museums and natural history collections were of vital importance in completing this work. At the same time, though, museum data is imperfect. Below, I outline a few potential caveats that should be considered for any study that relies heavily on museum data.

First, with any historic records, there are inherent issues of specimen misidentification and taxonomic revisions over time. This type of error is relatively straightforward, and can often be addressed by either physically examining each specimen (assuming good preservation since collection), or using genetic techniques to identify degraded specimens or highly cryptic species. Unfortunately, examining every specimen may be too time consuming for studies using several thousand records from diverse museum collections. For these larger scale studies, removing records that occur well outside the established range, or updating a species' name when taxonomic revisions are based on geographic criteria, are ways of mitigating some potential errors in a large data set when directly examining each specimen is unfeasible.

Of greater importance for most studies are issues inherent in the nature of museum data. First, where species have been collected depends heavily on where people doing the collecting are located. This leads to potential geographic biases, as accessibility to a site increases the likelihood of collection. Numerous studies have found that species occurrence records are clustered around towns, rivers, roadways, universities, and field stations (Hijmans et al. 2000). Also, areas with a strong history of interest in natural history collections, such as Western Europe, often have far more numerous and older records than areas where museum collections have only been more recently established.

Because of these inherent biases in where records have been collected, comparisons between geographic regions must take difference in collection effort into account.

Second, the motivation of collectors and the collection methods used introduce an additional source of bias. If a collector's goal is to complete a life list or add unusual specimens to a collection, rare species could be disproportionally collected compared to their relative abundance simply because they are rare and therefore interesting to collectors. Weedy or other highly abundant species, at the same time, may be under-collected relative to their abundance simply because their abundance renders them 'uninteresting'. Collection methodologies may also vary between collectors and over time as new techniques are introduced and become common. For example, the use of firearms in collecting mammals has become less common in recent collection (Myers et al. 2009). Both this potential bias towards collecting rare species and a difference in collection methodologies means that it can be difficult to make inferences about a species' relative abundance (Myers et al 2009). Therefore, reconstructing species assemblages or calculating species richness using only museum data is extremely difficult. Studies using museum collections to draw conclusions about species diversity and richness must carefully consider how to correct for these differences in sampling effort, as the methodology used may greatly influence the outcome (Fagan and Kareiva 1997).

Third, locality information is important for biogeographical studies, but this data, especially for older specimens, may be quite vague or contain internal inconsistencies (Chapman and Wieczorek 2006). While this problem has been substantially improved by the increased use of handheld GPS units, difficulty interpreting locality data can be a

major issue for older specimens. Indeed, the vast majority of specimens at many major museums and repositories are not yet georeferenced, and updating collections requires a substantial investment of time and effort. An additional issue that can occur even when the locality of a record was collected carefully and accurately is that human landmarks are most often used as reference points (i.e. distance from a road intersection or from a town center), yet the location of these landmarks may change over time or disappear completely. For example, many towns used as reference points in the American southwest in the 1800's and early 1900's are now 'ghost towns', and can be extremely difficult to track down using current georeferencing practices (pers. obs.).

Finally, by its nature, museum data is considered 'presence-only' data. A lack of any specimen from a particular time or place may mean that a species was not present. However, absence data could also reflect a lack of collection effort. Disentangling whether a new occurrence record of a species represents a true range expansion or instead simply reflects the first collection from a previously unsampled area can be difficult (Frey 2009). This may be a particular problem at range edges, where species are expected to be rare and thus less likely to be observed and collected (Chapter 5). Because of this issue, using past data to reconstruct historic ranges is particularly difficult. One possible means of correcting for this issue in future collections is for collectors to note what other species, if any, are present at the time of collection. Although this may be more time consuming for collectors, it will potentially provide invaluable information regarding species assemblages at a given time and location.

Given all these caveats, what is museum data good for? Even with the bias inherent in museum records, these data are still an immensely useful source of

information about when and where species have been collected. Records from museums have been used to track the spread of invasive species over time (e.g. Ward 2007) and to document distributional changes due to climate change (e.g. Myers et al. 2009). Museum specimens also provide species occurrence records that can be used in ecological niche modeling, a method for predicting species distributions (Graham et al. 2004). Finally, genetic information from museum specimens has been very useful both in the fields of conservation genetics and evolution (Wandeler et al. 2007).

While all studies using museum specimens should explicitly address how potential biases can influence the conclusions that can be drawn, museum specimens are an important source of data. As anthropogenic disturbance increasingly affects species across the globe, there is an increased need for natural history to be collected in a way that is easily accessible to scientists.

In summary, my goal was to illustrate how studying environmental heterogeneity at different biological and geographic scales contributes to our understanding of evolution and ecology. While important questions remain in this field, this work will hopefully provide a foundation from which future empirical studies can be based.

REFERENCES

Brown, W. L. and E. O. Wilson. 1956. Character displacement. Systematic Zoology 5: 49-64.

Chapman, A. D. and J. Wieczorek (eds). 2006. Guide to Best Practices for Georeferencing. Copenhagen: Global Biodiversity Information Facility.

Fagan, W. F. and P. M. Kareiva. 1997. Using compiled species lists to make biodiversity comparisons among regions: A test case using Oregon butterflies. Biol. Cons. 80: 249-259.

Frey, J. K. 2009. Distinguishing range expansions from previously undocumented populations using background data from museum records. Diversity Distrib. 15: 183-187.

Gause, G. F. 1934. *The struggle for existence*. Williams and Wilkins, Baltimore, Maryland, USA.

Graham, C. H., S. Ferrier, F. Huettman, C. Moritz, and T. Peterson. 2004. New developments in museum-based informatics and applications in biodiversity analysis. Tree 19: 497-503.

Gray, S. M. and J. S. McKinnon. 2007. Linking color polymorphism maintenance and speciation. Trends Ecol. Evol. 22: 71-79

Hardin, G. 1960. The competitive exclusion principle. Science 131, 1292-1297.

Hijmans, R. J., K. A. Garrett, Z. Huaman, D. P. Zhang, M. Schreuder, M. Bonierbale. 2000. Assessing the geographic representation of genebank collections: The case of the Bolivian wild potatoes. Conserv. Biol. 14, 1755-1765.

Hochkirch, A., Gröning, J. & Bücker, A. 2007 Sympatry with the devil: Reproductive interference could hamper species coexistence. J. Anim. Ecol. 76, 633-642.

Hsieh, C.-H., H. J. Kim, W. Watson, E. D. Lorenzo, and G. Sugihara. 2009. Climate-driven changes in abundance and distribution of larvae of oceanic fishes in the southern California region. Global Change Biol.

Myers, P., B. L. Lundrigan, S. M. G. Hoffman, A. P. Haraminac, and S. H. Seto. 2009. Climate-induced changes in the small mammal communities of the Northern Great Lakes Region. Global Change Biology. 15: 1434-1454.

Slatkin, M. 1980. Ecological character displacement. Ecology 61, 163-177.

Wandeler, P., P. E. A. Hoeck, and L. F. Keller. 2007. Back to the future: museum specimens in population genetics. TREE 22: 634-642.

Ward, D. 2007. Modelling the potential geographic distribution of invasive ant species in New Zealand. Biol. Invasions. 9: 723-735.